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Revision of Australo-Papuan *Pipistrellus* and of *Falsistrellus* (Microchiroptera: Vespertilionidae)

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Abstract

A classical morphological taxonomic approach has been used to clarify the status of Australian and New Guinea species usually placed in the genus *Pipistrellus*. Multivariate phenetic and phylogenetic analyses of a suite of morphological characters were undertaken to determine the relationships between the taxa recognised in this study.

In tropical Australia, *Pipistrellus tenuis westralis* Koopman, 1984, from coastal and near coastal Kimberley, Northern Territory and western Queensland is elevated to species status. *Pipistrellus adamsi* sp. nov. is described from north Queensland and Northern Territory.

In New Guinea the following species of pipistrelles are recognised: *P. papuanus* (Peters and Doria, 1881); *P. angulatus* Peters, 1880; *P. collinus* Thomas, 1920 — as well as *P. wattsi* sp. nov. which is described from southeastern coastal New Guinea.

In more southern parts of Australia two species are recognised and placed in the genus *Falsistrellus* Troughton, 1943 [*F. tasmaniensis* (Gould, 1858) and *F. mackenziei* sp. nov.]. The former species is from Tasmania, Victoria, New South Wales and southeastern Queensland and the latter is described from southwestern Western Australia.

The phylogenetic and phenetic analyses support the generic distinction between *Falsistrellus* and *Pipistrellus* and suggest that the northern Australian pipistrelles have evolved independently from New Guinea species.

Introduction

Named forms considered in detail in this study are those that have been recorded from Australia, Papua New Guinea and Irian Jaya. These are *Pipistrellus tasmaniensis* (Gould, 1858) — southern Australia including Tasmania; *P. krefftii* (Peters, 1869) — New South Wales; *P. angulatus* Peters, 1880 — Papua New Guinea and its southeastern islands; *P. papuanus* (Peters and Doria, 1881) — northwestern Irian Jaya, Papua New Guinea, Queensland; *P. papuanus orientalis* Meyer, 1899 — northeastern Papua New Guinea; *P. papuanus collinus* Thomas, 1920 —highland Papua New Guinea; *P. ponceleti* Troughton, 1936 — Papua New Guinea, southeastern islands; and *P. tenuis westralis* Koopman, 1984 — Kimberley, Western Australia.

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Other species considered are *P. tenuis tenuis* (Temminck, 1840), *P. javanicus* (Gray, 1838) and *P. imbricatus* Horsfield, 1824. The type locality of *P. t. tenuis* is Sumatra, Indonesia. The distribution of *P. javanicus* includes South Assuri region (USSR), Korea, Japan, China and South East Asia to Java and the Philippines (Honacki *et al.* 1982); two specimens of *P. javanicus* reported from Australia (Dobson 1878) have been examined and confirmed as *P. javanicus* by Hill (1983), Koopman (1984) and by us, but there remains considerable doubt as to their collection locality. *P. imbricatus* occurs in Java, Kangean I., Bali I. and Palawan, Luzon and Negros Is (Philippines) (Honacki *et al.* 1982). Lidicker and Ziegler (1968) report a possible record of *P. imbricatus* from Papua New Guinea and from Emirau I., Bismark Archipelago, which is not confirmed (see Hill 1983).

Pipistrellus regulus Thomas 1906, from southwestern Australia, was reported by Hill (1966) to be an *Eptesicus*. It is now recognised as *Eptesicus regulus* (Kitchener and Halse 1978).

There has been considerable shuffling in the taxonomic status of these principal named forms by the major reviewers. Tate (1942) recognised all those named at that time as valid taxa but elevated *collinus* to species rank and placed *krefftii* as a subspecies of *P. tasmaniensis*. Laurie and Hill (1954) considered both *collinus* and *ponceleti* as subspecies of *P. angulatus* and *orientalis* as synonymous with *P. papuanus*. Lidicker and Ziegler (1968) largely followed Laurie and Hill (1954), but tentatively considered *ponceleti* as a species and more closely related to *P. imbricatus* than to *P. angulatus*, but not to *P. papuanus* as suggested by Troughton (1936). Koopman (1973) considered *angulatus, collinus, ponceleti* and *papuanus* to be subspecies of *P. tenuis* (Temminck, 1840). McKean and Price (1978) documented substantial morphological differences between bacula of these latter forms, but followed Koopman (1973) in considering them as subspecies of *P. tenuis*. Koopman (1984) described *P. tenuis westralis*.

Miller (1907) diagnosed *Pipistrellus*, which at that time included about 40 species, as having the dental formula: $I\frac{2\text{-}2}{3\text{-}3}$, $C\frac{1\text{-}1}{1\text{-}1}$, $P\frac{2\text{-}2}{2\text{-}2}$, $M\frac{3\text{-}3}{3\text{-}3}$; I^2 not as large as I^1, but extending considerably beyond its cingulum; I^1 simple, or more often with a well developed secondary cusp (as in *P. pipistrellus*). Canines usually rather stout, posterior cutting edge of C^1 usually with incipient secondary cusp; P^2 barely or not in tooth row. In 1829 Kaup (see Tate 1942:234) characterised *Pipistrellus* (then consisting of *Vespertilio pipistrellus* Schreber, 1774 and *V. kuhlii* Kuhl, 1819) as having short simple ears with bases far apart, tragus short and arched inwards, and 32 teeth.

Tate (1942) defined *Pipistrellus* as a short faced Vespertilioninae in which the dental formula is $I\frac{2}{3}$, $P\frac{2}{2}$. He considered that no uniform unspecialised pipistrelle existed —incisors, canines or premolars have in every species acquired peculiarities. He considered that ideally the upper incisors should be subequal in size, each with accessory cusps well set off; lower incisors scarcely thickened and linearly arranged; canines without accessory cusps; P^2 not smaller than I^2, slightly or not displaced inwards from tooth row, leaving an obvious diastema between C^1 and P^4. P_2 slightly smaller than

P_4, retained in tooth row. M^3_3 remains unmodified in all species of *Pipistrellus.* Tate (1942) recognised 14 species groups of *Pipistrellus;* an arrangement that he considered 'unsatisfactory' because these groups present a complex of 'archaic and specialised structures'.

The named forms dealt with in this revision fall into three of Tate's (1942) groups as follows:

(i) *Pipistrellus coromandra* group — perhaps nearest to the group with type species *(P. pipistrellus)* but with less depressed rostrum and less full braincase; dentition virtually as in *Pipistrellus pipistrellus* with P^2_2 little reduced and lower incisors scarcely imbricated; posterior canine cusp usually present. Includes *P. imbricatus, P. angulatus, P. collinus* and *P. ponceleti.*

(ii) *Pipistrellus tenuis* group — smallest species with radius lengths 27-30 mm; premaxilla exceptionally short; zygoma weak; braincase full, short; frontal region rather steep; rostrum low, somewhat as in *P. pipistrellus;* some broadening of muzzle; P^2 about half area of I^2. Includes *P. tenuis, P. papuanus* and *P. papuanus orientalis.*

Tate (1942) distinguished the *P. coromandra* and *P. tenuis* groups by their unshortened premaxilla, relatively narrower palate and less globular braincase, but noted that the "New Guinea forms *papuanus, angulatus* and *collinus* bridge the gap" between these two groups.

(iii) *Pipistrellus tasmaniensis* group — Tate considered this group 'distinctly aberrant'; distinguished from most pipistrelles by unicuspid I^1 and presence of occipital helmet; P^2_2 much reduced; zygoma weak. Includes *P. tasmaniensis* and *P. krefftii.*

Ellerman and Morrison-Scott (1951) reviewed more recent taxonomic appraisals of *Pipistrellus.* They concluded that "strictly speaking *Pipistrellus* is not more than a subgenus of *Eptesicus,* which itself might be referred to *Vespertilio*". This conclusion was based, in the main, on the unreliability of the presence of P^2 as a diagnostic generic character for *Pipistrellus.* However, for convenience only, these authors followed Miller (1907) and Tate (1942) in their treatment of *Pipistrellus,* also incorporating *Scotozous,* as did Honacki *et al.* (1982). Hill (1976), however, considered *Scotozous* to be transitional between *Pipistrellus* and the 'nycticeine' genera of Tate (1942).

The dubious nature of the presence or absence of P^2 to distinguish between *Pipistrellus* and *Eptesicus* is further discussed by Hill and Topál (1974) and Kock (1969) who point out that in several species, presence of P^2 varies intraspecifically. Unfortunately no other diagnostic morphological characters additional to P^2 have been discovered to distinguish *Pipistrellus* and *Eptesicus* (Koopman 1975, Heller and Volleth 1984). The latter authors pointed out that classifications based on this tooth character "may well prove to misrepresent natural relationships"; they suggest de-emphasising the importance of P^2 and focusing on karyotype and bacula. While these characters allow them to readily characterize *Eptesicus* (after the Australian species are removed from this genus) (50 chromosomes, small non stick-like baculum) and *Vespertilio* (38 chromosomes, baculum position either in middle of penis or basal with an additional long pseudobaculum), the situation with *Pipistrellus* is still obscure. In *Pipistrellus* both the size of bacula (most more or less stick-like) and number of chromosomes (26-44) show considerable differences which lead them to suggest that "a closer examination may possibly justify splitting the genus".

Of the Australo-Papuan *Pipistrellus,* there has been most confusion as to the generic placement of *P. tasmaniensis.* Iredale and Troughton (1934) placed it in *Glischropus,* but it clearly has no place in this genus (see Tate 1942). As noted, Tate (1942) drew attention to its distinctive characteristics and Troughton (1943) erected the new genus *Falsistrellus* to accommodate it. The brief diagnosis for *Falsistrellus* distinguishes it from *Pipistrellus* by having the minute unicuspid I^2 rotated so that the normal hindward convexity is turned outwards against the canines. In this revision we concur with Troughton (1943) and consider that there is sufficient morphological (and electrophoretic evidence, M. Adams pers. comm.) to warrant generic distinction between *tasmaniensis* and the other small pipistrelles that we include in this study.

As noted earlier, the northern Australian and Papua New Guinea species we studied belong to the *P. coromandra* and *P. tenuis* groups or are annectant between these groups (Tate 1942). Both these groups, particularly *P. coromandra* are most similar to the *Pipistrellus pipistrellus* group and we consider them representative of *Pipistrellus (sensu stricto).*

Our detailed re-diagnosis of *Falsistrellus* is compared with the other small *Pipistrellus* considered herein. We make no attempt to compare it in detail with *Pipistrellus (sensu lato)*; such a comparison would appear to be unprofitable at this juncture because the available evidence suggests strongly that the remaining pipistrelles are not a monophyletic group.

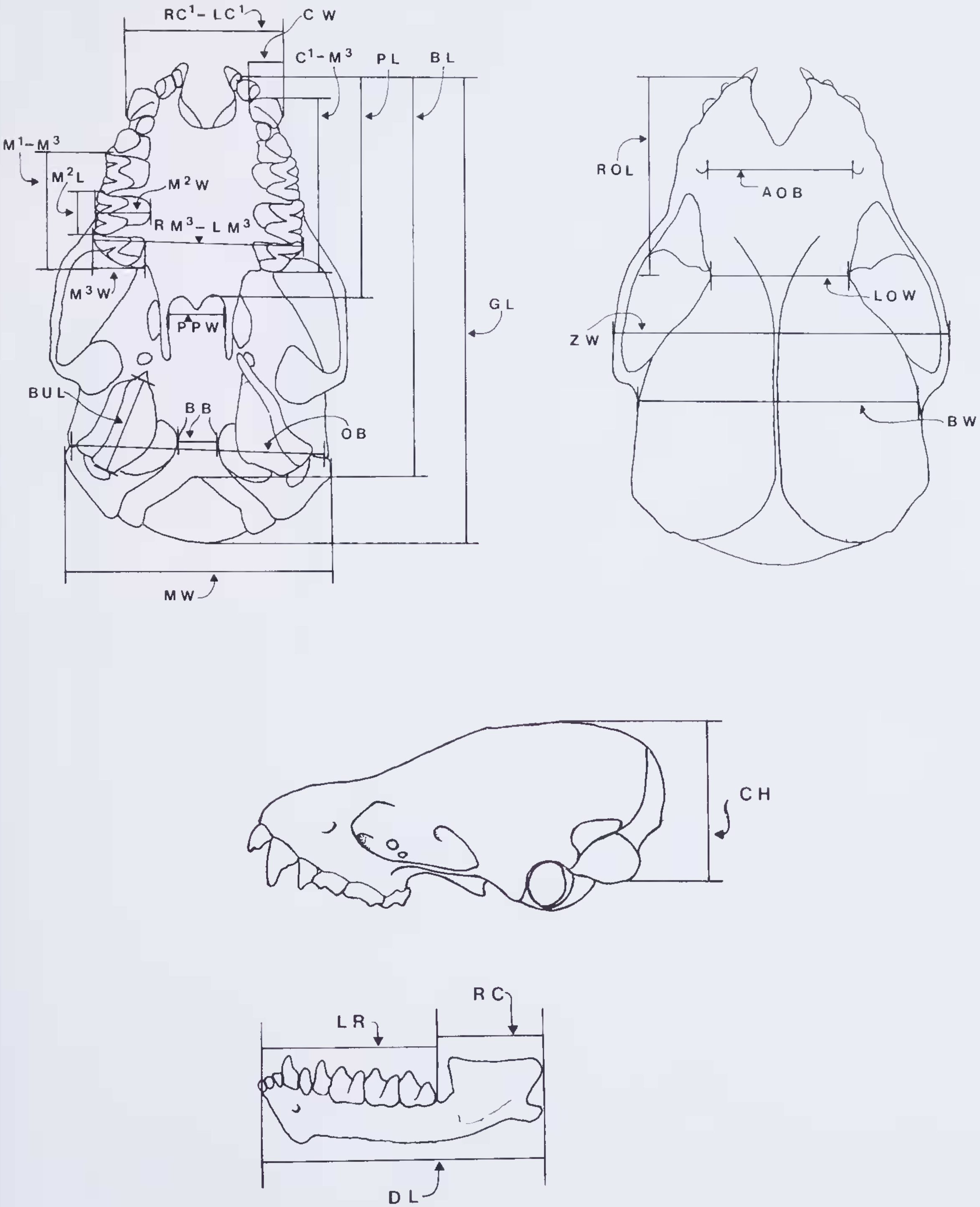
Methods

Morphology

Teeth — terminology of tooth structure follows Slaughter (1970) and is illustrated for upper and lower molars in Kitchener and Caputi (1985).

Skull, dentary and externals — twenty five measurements (in mm) of skull and 12 of external characters were recorded, from adult specimens only; these are listed in the sections 'Specimens Examined', measurements of holotypes and unique specimens are listed in Appendix I. Subadults and juveniles were diagnosed on the basis of epiphyseal swellings of the metacarpal joints. The terminology used follows Kitchener and Caputi (1985). Colours of pelage and skin are capitalised where they follow the Ridgeway (1912) colour charts.

All measurements were recorded with dial calipers. The positions of these measurements are indicated in Figure 1.


RC^1-LC^1
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C^1-M^3
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BL
M^1-M^3
M^2L
M^2W
RM^3-LM^3
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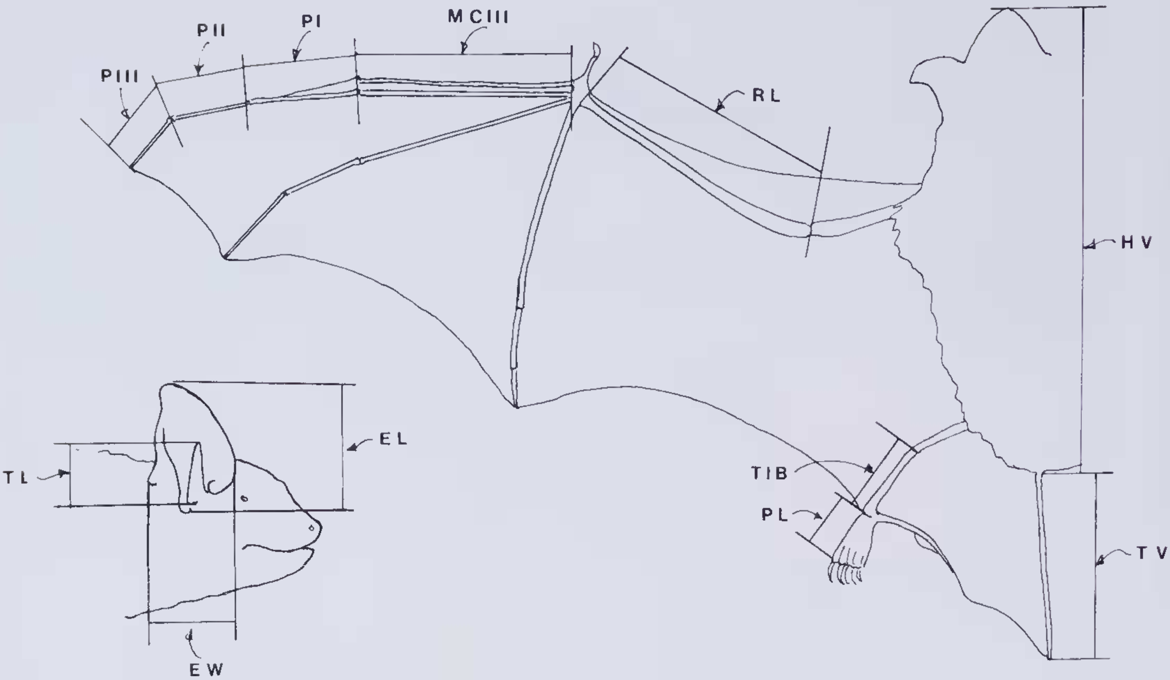


Figure 1 Skull, dentary and external body measurements referred to in text and their recording points. GL: greatest skull length; AOB: anteorbital width, between infraorbital foramina; LOW: least interorbital width; ZW: zygomatic width; ROL: rostrum length, from LOW to anterior edge of premaxilla; MW: mastoid width, between mastoid processes; BW: braincase width, at centre of zygomatic-squamosal contact; CH: cranial height, lower arm of calipers placed level with pre- and basisphenoid, upper arm in contact with apex of skull; PL: palatal length, excluding postpalatal spine; PPW: postpalatal width; BL: basicranial length, between anterior edge of foramen magnum and anterior edge of premaxilla; BUL: bulla length, excluding eustachian part; BB: width of basisphenoid between cochlea; OB: distance outside bullae, caliper points in contact with antero-dorsal edge of tympanic ring; CW: canine width, maximum diameter at base; RC^1-LC^1: inter upper canine distance, at base of cusp; C^1-M^3: upper maxillary tooth row crown length, anterior edge of C^1 to posterior edge M^3; M^1-M^3: upper molar crown length, anterior edge M^1 parastyle to posterior edge M^3; M^2L: upper second molar crown length, anterior edge of parastyle to posterior edge of metastyle; M^2W: upper second molar crown width, lingual base of protocone to buccal face of paracone, at right angles to occlusal surface; M^3W: upper third molar crown width, as for M^2W; RM^3-LM^3: inter upper third molar distance, across buccal face of paracone of RM^3 and LM^3; LR: lower tooth row, posterior edge M_3 to anterior edge of dentary; RC: angular ramus to dentary condyle, blade caliper along anterior face of ramus and measuring to posterior edge of articular condyle; DL: dentary length, from condyle to anterior tip of dentary; HV: body length, tip of rhinarium to anus. TV: tail length, tip to anus; EL: ear length, apex to basal notch; EW: ear width across basal lobes; TL: tragus length; RL: radius length; MC III: metacarpal III length; PI: digit III, phalanx I length; PII: digit III, phalanx II length; PIII: digit III, phalanx III length; TIB: tibia length and PL: pes length.

Morphometric Analyses

Sexual dimorphism was examined using a two factor analysis of variance for measurements of each of the skull, dentary, teeth (skull characters) and external characters for the factors-species and sex.

Canonical variate (discriminant) analyses, using both the skull and external measurements, were performed for each species using SPSS (Nie *et al.* 1975) and GENSTAT Package, Rothamsted Experimental Station. To obtain an unbiased estimate of the correct classification rate, the canonical variate analyses were repeated using only a randomly chosen 90 percent of the specimens; the canonical variate funtions so obtained were then used to classify the remaining 10 percent of the specimens.

In some of the canonical variate analyses, a Mahalanobis distance matrix was obtained and subjected to a minimum spanning tree analysis and a hierarchical cluster analysis using the unweighted pair group mathematical averaging method (UPGMA).

Cladistic analyses were performed using the Wagner 78 program for constructing trees. These analyses were based on the mean values (range coded) of the skull and external characters of the specimens in the species.

The above analyses, canonical variate analyses, minimum spanning tree, cluster analyses and cladistic analyses were also performed after attempting to correct for size in the 37 variables. This was done by a principal component analysis of the within-species correlation matrix on the skull and external variables. The latent vectors of this analysis were then examined to determine if the first (and second) vectors had values which suggested that the vector(s) were size vectors. If this was the case then the PC scores associated with these vectors were omitted from the canonical variate and other analyses.

Institutional Specimens

To denote the institutional origin of specimens, their catalogue numbers are prefixed by the following abbreviations:

A : Hobart Museum
AM : Australian Museum, Sydney
AMNH : American Museum of Natural History, New York
BM : British Museum (Natural History), London
C : Museum of Victoria, Melbourne
CM : CSIRO Wildlife Collections, Canberra
JM : Queensland Museum, Brisbane
MSNG : Museo Civico di Storia Naturale, Genova
QVM : Queen Victoria Museum, Tasmania
SAM : South Australian Museum, Adelaide
WAM : Western Australian Museum
EBU : Evolutionary Biology Unit, South Australian Museum, Adelaide

Systematics

Falsistrellus Troughton, 1943

Falsistrellus Troughton, 1943: 'Furred Animals of Australia', Angus & Robertson, Sydney.

Type Species
Falsistrellus tasmaniensis (Gould, 1858)

Referred Species
Falsistrellus mackenziei sp. nov.

Diagnosis (mean values)

Falsistrellus differs from *Pipistrellus (sensu stricto),* as reflected by the following species of *Pipistrellus: westralis, adamsi* sp. nov., *papuanus, wattsi* sp. nov., *angulatus* and *collinus,* in being considerably larger in all measurements. Comparison between selected measurements of the small species of *Falsistrellus (tasmaniensis)* and the largest of the representative *Pipistrellus* positively identified in the Australian zoogeographic region *(P. collinus)* are as follows: greatest skull length (18.3 v. 13.2), mastoid width (10.3 v.7.5), C^1-M^3 (7.1 v. 4.7), dentary length (13.9 v. 9.4), radius length (50.8 v. 37.2), tibia length (21.9 v. 15.4); narrower braincase with parietal less inflated laterally such that braincase narrower relative to greatest skull length (0.48 v. 0.52); dorsal profile of skull flatter; marked occipital crest formed by prominent sagittal and lambdoidal crest — these crests are absent or much weaker in *Pipistrellus;* posterior apex of skull projects further posteriorly, usually beyond supraoccipital; supraorbital tubercles much more prominent, linked by much more prominent crests to sagittal crest in interorbital region; glenoid surface for mandibular condyle wider than long rather than subcircular or square; I^1 unicuspid rather than bicuspid; I^2 very small, barely above height of I^1 buccal cingulum rather than approximately half to two-thirds height of I^1; I^2 swivelled such that it is outside the line of the tooth row against the posterolateral surface of I^1, rather than little or not extruded from line of tooth row; M^{1-2} hypocone more developed: P^4 anterolingual cusp small to absent rather than well developed; C^1 broad at base rather than narrowly elongate; C^1 lingual cingulum more prominent with more prominent cusplets; lower incisors imbricate, close contact, rather than not imbricate and frequently not in contact; P_2 much smaller, less than half crown area and half height of P_4 rather than greater than three-quarters crown area and more than half height of P_4; M_{1-3} first triangle subequal to, rather than considerably smaller than, the second triangle; coronoid process of mandible more erect, length of posterior edge subequal to anterior edge rather than much longer; rectangular-shaped baculum without bifurcated distal end and without narrow shaft and obviously broader basal part; glans penis short and broader with wider flanges and no prominent distal lobe or fleshy spines; line of supratragus projected posteriorly, meets tragus at approximately its mid point, rather than two-thirds up its length. Differs at an average of 80 percent of the 36 allozyme loci examined (M. Adams pers. comm.).

Differs from *Pipistrellus (sensu lato)* by its larger size (Tate 1942), I^2 small and swivelled outwards against I^1, such that it is extruded from the line of tooth row (Troughton 1943); and a combination of unicuspid I^1, tiny P^2 and pronounced occipital crest (Tate 1942).

Falsistrellus tasmaniensis (Gould, 1858)

Figures 2, 3, 4, 5a, 6a, 7, 17; Tables 1 and 2

Vespertilio tasmaniensis Gould, 1858 (1863): Mammals of Australia, III. Pl. XLVIII (with text).

Vesperugo krefftii Peters, 1869: Mber. K. Preuss Akad. Wiss., p. 404, New South Wales.

Holotype

BM43.2.22.6, skin and partial skull (with only rostrum and toothrows), from Tasmania.

Diagnosis (mean values)

Differs from *F. mackenziei* by being generally smaller: greatest skull length (18.3 v. 19.2), zygomatic width (12.4 v. 13.2), braincase width (8.8 v. 9.1), mastoid width (10.3 v. 10.5), palatal length (8.9 v. 9.2), digit III, phalanx I (18.8 v. 20.2); dentary shorter relative to basicranial length (Figure 2); glans penis generally both slightly smaller and with dorsal hump and lateral wings reduced; baculum longer for any given basal width (Figure 3), without notched basal dorsal ridge. Specimens not distinguished on the above may be allocated by using the discriminant functions detailed later.

Description (mean and range)

Skull and Dentary (Figure 4)

Large robust skull: greatest length 18.3 (17.5-19.0), zygomatic width 12.4 (11.6-13.0), interorbital width 5.0 (4.7-5.3), braincase width 8.8 (8.3-9.2), mastoid width 10.3 (9.4-10.7); dorsal skull profile relatively flat, frontals rising only slightly in interorbital region; anterior nares shape reaching posteriorly to a line joining anterior edge or centre of infraorbital foramina; supraorbital tubercles slight to small; infraorbital foramen moderate to large, subcircular, above M^1 parastyle, separated from orbit by narrow to moderate lachrymal bar; zygoma weak; anteropalatal emargination spatulate, extends to P^2; palatal depression moderate; postpalatal width moderate 2.1 (1.9-2.4); postpalatal spine moderate, broadly triangular; pterygoid processes moderate, broadly triangular, posterior edge concave; sphenorbital sinus elongate, extends well anterior to posterior margin of palate; bulla length moderate 3.6 (3.3-3.9), cover *c.* two-thirds cochlea, eustachian part short, blunt; median sphenoid depression slight to absent; basisphenoid pits moderate to shallow; P^2 tiny, less than half size I^2, level with or slightly lower than C^1

cingulum; P^4 buccal edge slightly notched, two-thirds height C^1; M^{1-3} paracrista increasing in length posteriorly; metacrista M^{1-2} subequal; M^3 with obvious paracrista, postparacrista and premetacrista but with mesostyle and metacone greatly reduced, metacrista and metastyle absent; paracone and metacone decrease in height from M^{1-3}; moderate cingula encircle I^1 and I^2 (except for the region of contact with I^1), as well as C^1 and P^4; buccal cingula absent M^{1-3}; slight posterior cingula M^{1-2}; small to moderate

Table 1a, b. Measurements in mm (see Figure 1 for code to characters), for adult *Falsistrellus tasmaniensis, F. mackenziei, Pipistrellus westralis, P. adamsi, P. papuanus, P. wattsi, P. angulatus, P. collinus, P. javanicus* and *P. imbricatus*. N, sample size; x̄, mean; SD, standard deviation; Mn, minimum and Mx, maximum, (a) skull, dentary and teeth and (b) externals.

Table 1a

		Skull, Dentary and Teeth Characters																								
		GL	AOB	LOW	ZW	ROL	MW	BW	CH	PL	PPW	BL	BPL	BB	OB	CW	RC^1LC^1	C^1M^3	M^1M^3	M^1L	M^1W	M^3W	RM^3LM^3	LR	RC	DL
F. tasmaniensis	N	56	56	56	52	54	51	56	55	56	56	56	52	56	56	56	56	56	56	56	56	56	56	55	55	55
	x̄	18.3	6.1	5.0	12.4	7.7	10.3	8.8	6.9	8.9	2.1	16.1	3.6	1.9	9.1	1.1	6.2	7.1	4.7	1.7	2.0	2.1	7.9	8.4	4.1	13.9
	SD	0.39	0.22	0.13	0.31	0.31	0.27	0.19	0.21	0.26	0.09	0.43	0.15	0.15	0.18	0.06	0.22	0.17	0.11	0.06	0.09	0.09	0.21	0.21	0.16	0.34
	Mn	17.5	5.7	4.7	11.6	7.0	9.4	8.3	6.4	8.2	1.9	15.1	3.3	1.6	8.7	0.9	5.6	6.8	4.4	1.6	1.8	1.8	7.4	7.9	3.8	13.0
	Mx	19.0	6.5	5.3	13.0	8.5	10.7	9.2	7.3	9.5	2.4	16.7	3.9	2.2	9.5	1.2	6.6	7.4	4.9	1.9	2.2	2.3	8.3	8.8	4.4	14.5
F. mackenziei	N	50	53	51	44	52	46	48	47	49	48	48	48	49	49	54	54	53	53	53	54	53	49	52	53	50
	x̄	19.2	6.5	5.0	13.2	8.0	10.5	9.1	7.4	9.2	2.2	16.5	3.7	2.0	9.5	1.2	6.7	7.4	4.9	1.9	2.3	2.2	8.4	8.9	4.4	14.8
	SD	0.42	0.20	0.14	0.38	0.27	0.29	0.21	0.23	0.27	0.12	0.41	0.13	0.16	0.21	0.09	0.22	0.15	0.13	0.08	0.11	0.09	0.20	0.18	0.16	0.32
	Mn	18.2	6.1	4.6	12.2	7.4	9.4	8.5	7.0	8.7	1.9	15.5	3.3	1.7	9.1	1.1	6.2	7.1	4.5	1.7	2.1	2.0	7.9	8.5	4.2	14.2
	Mx	20.1	6.9	5.2	13.9	8.7	11.0	9.6	8.0	9.8	2.4	17.4	4.0	2.2	9.9	1.4	7.1	7.8	5.2	2.0	2.5	2.4	8.8	9.3	5.0	15.6
P. westralis	N	18	16	17	7	18	18	18	17	18	17	18	18	18	18	18	16	18	18	18	18	18	17	17	18	17
	x̄	11.4	3.6	3.6	7.5	4.7	6.7	6.2	4.3	5.1	1.6	9.5	2.6	1.1	6.1	0.5	3.6	3.9	2.5	1.0	1.2	1.2	5.0	4.8	2.2	8.0
	SD	0.23	0.14	0.20	0.17	0.18	0.16	0.17	0.13	0.17	0.11	0.20	0.11	0.12	0.13	0.05	0.14	0.11	0.11	0.03	0.06	0.07	0.13	0.12	0.10	0.17
	Mn	11.1	3.4	3.3	7.3	4.4	6.4	5.9	4.1	4.8	1.5	9.0	2.3	0.8	5.9	0.4	3.4	3.7	2.3	0.9	1.1	1.1	4.8	4.5	2.0	7.7
	Mx	11.9	3.9	3.9	7.8	5.0	7.0	6.5	4.7	5.3	1.9	9.9	2.7	1.3	6.4	0.6	3.8	4.1	2.7	1.0	1.3	1.3	5.2	5.0	2.4	8.2
P. adamsi	N	18	19	19	10	19	20	20	20	20	20	20	20	20	20	20	19	20	20	20	20	20	19	20	20	20
	x̄	12.0	4.0	3.7	8.1	5.4	7.1	6.4	4.6	5.6	1.5	10.1	2.7	1.4	6.5	0.57	4.2	4.4	2.8	1.1	1.3	1.3	5.5	5.4	2.5	8.9
	SD	0.24	0.11	0.11	0.07	0.21	0.12	0.15	0.16	0.17	0.06	0.25	0.08	0.10	0.14	0.06	0.13	0.13	0.08	0.05	0.06	0.06	0.12	0.13	0.08	0.14
	Mn	11.7	3.8	3.6	8.0	5.0	6.9	6.2	4.3	5.4	1.3	9.7	2.6	1.2	6.2	0.4	3.9	4.1	2.7	1.0	1.2	1.2	5.3	5.2	2.3	8.7
	Mx	12.6	4.2	3.9	8.2	5.7	7.3	6.7	5.0	6.0	1.5	10.5	2.8	1.5	6.8	0.6	4.3	4.6	3.0	1.2	1.4	1.4	5.7	5.7	2.6	9.3
P. papuanus	N	27	27	27	17	27	27	27	27	27	26	26	27	27	27	27	27	27	27	27	27	27	27	27	27	27
	x̄	11.9	3.7	3.5	7.9	5.1	7.0	6.3	4.5	5.2	1.7	9.8	2.6	1.3	6.3	0.59	4.0	4.1	2.7	1.0	1.3	1.3	5.4	5.1	2.5	8.4
	SD	0.34	0.16	0.12	0.20	0.26	0.20	0.18	0.14	0.19	0.10	0.31	0.12	0.13	0.15	0.06	0.14	0.14	0.11	0.05	0.08	0.06	0.18	0.15	0.10	0.24
	Mn	11.1	3.4	3.3	7.6	4.5	6.6	6.0	4.2	4.8	1.4	9.2	2.4	1.0	6.0	0.5	3.6	3.8	2.4	0.9	1.0	1.2	5.1	4.6	2.2	8.0
	Mx	12.5	4.0	3.7	8.3	5.7	7.4	6.9	4.7	5.6	1.8	10.4	2.8	1.7	6.6	0.7	4.2	4.4	2.9	1.1	1.3	1.4	5.7	5.3	2.6	8.9
P. wattsi	N	7	7	7	4	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7
	x̄	11.6	4.0	3.7	7.9	4.9	7.1	6.5	4.4	5.2	1.3	9.6	2.7	1.4	6.3	0.56	4.0	4.1	2.7	1.0	1.2	1.2	5.1	5.1	2.3	8.3
	SD	0.48	0.27	0.15	0.42	0.36	0.30	0.24	0.18	0.24	0.07	0.38	0.13	0.21	0.25	0.05	0.23	0.16	0.13	0.07	0.10	0.10	0.24	0.28	0.16	0.37
	Mn	11.1	3.5	3.5	7.1	4.4	6.4	6.1	4.2	5.0	1.2	9.2	2.5	1.0	5.9	0.5	3.6	3.9	2.5	0.9	1.1	1.0	4.8	4.8	2.1	7.8
	Mx	12.5	4.3	3.9	8.4	5.3	7.4	6.8	4.8	5.7	1.4	10.3	2.8	1.6	6.7	0.6	4.3	4.1	2.9	1.1	1.4	1.3	5.5	5.7	2.6	9.0
P. angulatus	N	18	18	19	14	18	19	19	19	18	18	17	19	19	19	18	17	18	19	19	19	19	18	18	18	18
	x̄	12.2	3.6	3.4	7.6	5.1	6.9	6.4	4.6	5.5	1.1	10.1	2.6	1.3	6.2	0.56	3.7	4.3	2.8	1.0	1.2	1.2	5.2	5.3	2.4	8.5
	SD	0.18	0.09	0.13	0.14	0.18	0.26	0.16	0.14	0.18	0.08	0.25	0.10	0.08	0.11	0.05	0.12	0.15	0.08	0.05	0.04	0.07	0.12	0.13	0.13	0.19
	Mn	11.9	3.1	3.2	7.3	4.8	6.6	6.1	4.3	5.1	1.3	9.6	2.5	1.2	6.0	0.5	3.5	4.0	2.6	1.0	1.1	1.1	5.0	5.0	2.1	8.1
	Mx	12.5	3.7	3.7	7.8	5.5	7.7	6.7	4.9	5.7	1.5	10.6	2.8	1.5	6.4	0.6	4.0	4.5	2.9	1.1	1.2	1.3	5.4	5.5	2.5	8.8
P. collinus	N	4	5	5	1	5	2	4	2	4	3	2	2	2	2	5	5	5	5	5	5	5	5	5	5	5
	x̄	13.2	4.1	3.5	8.8	5.3	7.5	6.8	5.0	6.0	1.6	11.3	3.1	1.3	7.1	0.80	4.2	4.7	3.1	1.3	1.4	1.5	5.8	6.0	2.8	9.4
	SD	0.32	0.22	0.21	—	0.45	0.14	0.10	0.07	0.26	0.15	0.14	0.07	0.28	0.07	0.07	0.28	0.18	0.07	0.05	0.07	0.08	0.24	0.07	0.17	0.22
	Mn	12.9	3.9	3.3	8.8	4.8	7.4	6.7	4.9	5.6	1.5	11.2	3.0	1.1	7.0	0.7	3.7	4.4	3.0	1.2	1.3	1.4	5.4	5.9	2.5	9.1
	Mx	13.5	4.4	3.8	8.8	5.9	7.6	6.9	5.0	6.2	1.8	11.4	3.1	1.5	7.1	0.9	4.4	4.9	3.2	1.3	1.5	1.6	6.0	6.1	2.9	9.7
P. javanicus	N	11	11	11	6	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	11	9	9
	x̄	13.1	4.4	3.7	8.7	5.5	7.5	6.8	4.8	6.1	1.8	11.0	2.9	1.3	7.0	0.9	4.4	4.9	3.1	1.2	1.4	1.5	5.9	6.0	2.8	9.5
	SD	0.34	0.14	0.18	0.35	0.22	0.25	0.24	0.15	0.27	0.15	0.40	0.13	0.15	0.17	0.05	0.13	0.18	0.13	0.07	0.05	0.04	0.11	0.19	0.16	0.34
	Mn	12.5	4.3	3.3	8.4	5.1	7.1	6.3	4.5	5.6	1.6	10.2	2.6	1.0	6.8	0.8	4.2	4.6	2.9	1.1	1.4	1.4	5.8	5.7	2.6	8.8
	Mx	13.4	4.7	4.0	9.4	5.9	7.9	7.1	5.1	6.4	2.1	11.5	3.1	1.5	7.4	0.9	4.7	5.2	3.3	1.3	1.5	1.5	6.2	6.3	3.0	9.9
P. imbricatus	N	7	7	7	5	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7
	x̄	12.4	4.1	3.6	8.5	4.2	7.2	6.8	5.0	5.2	1.4	10.2	3.0	0.74	7.1	0.89	4.3	4.2	3.0	1.2	1.5	1.5	5.4	5.4	2.7	8.7
	SD	0.23	0.14	0.10	0.38	0.10	0.36	0.24	0.11	0.26	0.11	0.21	0.13	0.10	0.36	0.07	0.08	0.22	0.12	0.05	0.07	0.05	0.25	0.24	0.16	0.30
	Mn	12.2	4.0	3.5	8.1	4.0	6.6	6.4	4.8	5.0	1.3	10.0	2.8	0.6	6.4	0.8	4.2	3.9	2.8	1.1	1.4	1.4	5.0	5.1	2.5	8.3
	Mx	12.8	4.3	3.7	8.9	4.3	7.7	7.0	5.1	5.7	1.6	10.5	3.2	0.9	7.4	1.0	4.4	4.6	3.1	1.2	1.6	1.5	5.8	5.8	2.9	9.1

Table 1b

Species		External Characters											
		HV	TV	EL	EW	TL	RL	MCIII	PI	PII	PIII	TIB	PL
F. tasmaniensis	N	43	39	43	44	44	42	42	43	44	44	42	43
	$\bar{x}$	62.3	47.0	17.0	10.7	9.4	50.8	47.9	18.8	15.0	12.9	21.9	10.1 .
	SD	2.47	2.29	1.00	0.61	0.56	1.44	1.35	0.70	0.74	0.76	0.77	0.82
	Mn	57.0	40.4	13.5	9.4	8.0	18.0	42.8	16.5	12.9	10.8	20.4	8.2
	Mx	66.3	51.2	19.1	11.8	10.5	56.3	50.0	20.1	16.2	14.4	23.5	11.9
F. mackenziei	N	48	45	48	18	18	41	44	48	47	48	48	48
	$\bar{x}$	61.7	46.2	16.7	10.8	9.2	50.7	47.8	20.2	14.9	12.4	22.1	10.2
	SD	2.28	2.83	0.98	0.58	0.63	1.24	1.35	0.78	0.70	0.74	0.77	0.69
	Mn	55.1	40.1	14.0	9.5	7.7	48.0	14.6	17.6	13.2	10.0	20.2	8.2
	Mx	66.6	53.2	18.3	12.2	10.6	53.7	50.0	21.7	16.2	13.6	23.6	11.6
P. westralis	N	29	28	31	31	30	30	30	31	31	30	29	30
	$\bar{x}$	37.0	31.5	10.0	7.5	5.0	28.9	28.0	11.0	8.9	6.5	11.9	4.9
	SD	1.89	1.76	0.63	0.52	0.29	0.86	1.00	0.43	0.55	0.87	0.45	0.30
	Mn	34.4	29.0	8.1	6.4	4.7	27.4	25.6	10.2	7.7	4.1	11.1	4.4
	Mx	42.2	37.2	11.0	8.5	6.1	30.3	29.5	11.9	10.0	8.4	12.6	5.7
P. adamsi	N	20	20	20	20	20	20	20	20	20	20	20	18
	$\bar{x}$	37.2	30.1	11.2	8.2	5.8	31.0	29.4	11.3	9.1	6.9	12.3	5.4
	SD	2.40	1.91	0.58	0.41	0.37	0.74	0.63	0.45	0.65	0.54	0.58	0.29
	Mn	33.9	26.7	9.4	7.6	5.2	29.8	28.2	10.6	8.4	6.1	10.7	5.1
	Mx	12.0	34.6	12.0	9.0	6.6	32.2	30.7	12.2	11.2	8.0	13.1	5.9
P. papuanus	N	25	24	26	26	26	26	26	26	26	26	26	26
	$\bar{x}$	38.6	28.3	10.5	7.4	5.2	29.7	27.7	10.2	8.7	6.2	12.0	5.5
	SD	2.11	2.12	0.88	0.63	0.57	1.02	1.27	0.65	0.64	0.53	0.65	0.40
	Mn	33.9	24.0	8.4	5.9	3.5	27.6	25.1	9.2	7.6	5.0	10.9	4.9
	Mx	11.8	32.7	11.8	8.2	5.9	31.9	30.2	11.1	10.1	7.1	13.2	6.5
P. wattsi	N	6	6	6	6	6	6	6	6	6	6	6	6
	$\bar{x}$	37.3	29.5	10.9	7.1	5.3	30.9	28.8	10.7	9.2	6.3	12.1	5.4
	SD	1.18	1.39	0.84	0.64	0.30	0.94	1.05	0.56	0.29	0.46	0.45	0.43
	Mn	36.0	27.6	10.0	6.7	4.8	29.6	27.1	9.9	8.7	5.6	11.7	4.8
	Mx	40.0	31.6	12.0	8.1	5.7	32.2	29.9	11.3	9.5	6.8	12.9	6.0
P. angulatus	N	15	16	16	16	16	16	16	16	16	16	16	16
	$\bar{x}$	38.2	32.1	11.2	7.7	5.7	32.8	31.1	12.3	10.6	7.0	13.5	5.9
	SD	2.22	2.48	0.65	0.54	0.30	1.03	1.20	0.51	0.64	0.76	0.36	0.39
	Mn	34.7	27.7	9.8	6.7	5.2	31.1	28.5	11.7	9.1	5.0	12.8	5.3
	Mx	41.4	36.0	12.1	8.8	6.3	34.8	32.9	13.3	11.5	8.2	11.0	6.7
P. collinus	N	—	—	—	—	—	3	3	3	3	3	3	3
	$\bar{x}$	—	—	—	—	—	37.2	34.5	13.5	11.3	7.4	15.1	7.6
	SD	—	—	—	—	—	1.74	1.14	0.91	0.84	0.27	1.12	0.97
	Mn	—	—	—	—	—	35.7	33.7	12.5	10.3	7.2	14.2	6 5
	Mx	—	—	—	—	—	39.1	35.8	14.2	11.8	7.7	16.4	8.4
P. javanicus	N	9	9	9	9	9	9	9	9	9	9	9	9
	$\bar{x}$	40.5	32.7	11.5	8.6	5.3	33.2	32.0	12.0	10.0	7.1	13.3	6.9
	SD	2.83	2.81	0.37	0.64	0.46	1.07	1.37	0.49	0.72	0.70	0.55	0.38
	Mn	36.9	27.7	10.9	7.7	4.4	31.7	30.8	11.3	8.8	5.8	12.2	6.4
	Mx	45.5	36.3	12.1	9.6	6.0	35.2	35.1	12.6	10.8	8.3	14.0	7.4
P. imbricatus	N	—	—	—	—	—	6	—	7	7	7	7	7
	$\bar{x}$	—	—	—	—	—	33.5	—	12.6	11.2	5.6	13.7	6.7
	SD	—	—	—	—	—	2.36	—	0.62	0.64	0.72	1.26	0.97
	Mn	—	—	—	—	—	29.0	—	11.1	10.1	4.8	11.6	5.4
	Mx	—	—	—	—	—	35.4	—	13.2	12.0	7.0	15.5	7.8

Table 2: Standardised and unstandardised canonical variates from *Falsistrellus tasmaniensis* and *F. mackenziei* for skull and external measurements with sexes combined (see Figure 1 for code to characters). Canonical variate scores are calculated as the summation of the products of the unstandardised canonical variates (in brackets) with their length measurements plus the constant.

Character	Variate I
CH	0.856 (4.100)
BL	-1.048 (-2.701)
BUL	-0.512 (-3.312)
CW	0.535 (7.103)
DL	1.542 (5.171)
PII	-0.803 (-1.173)
CONSTANT	-38.163

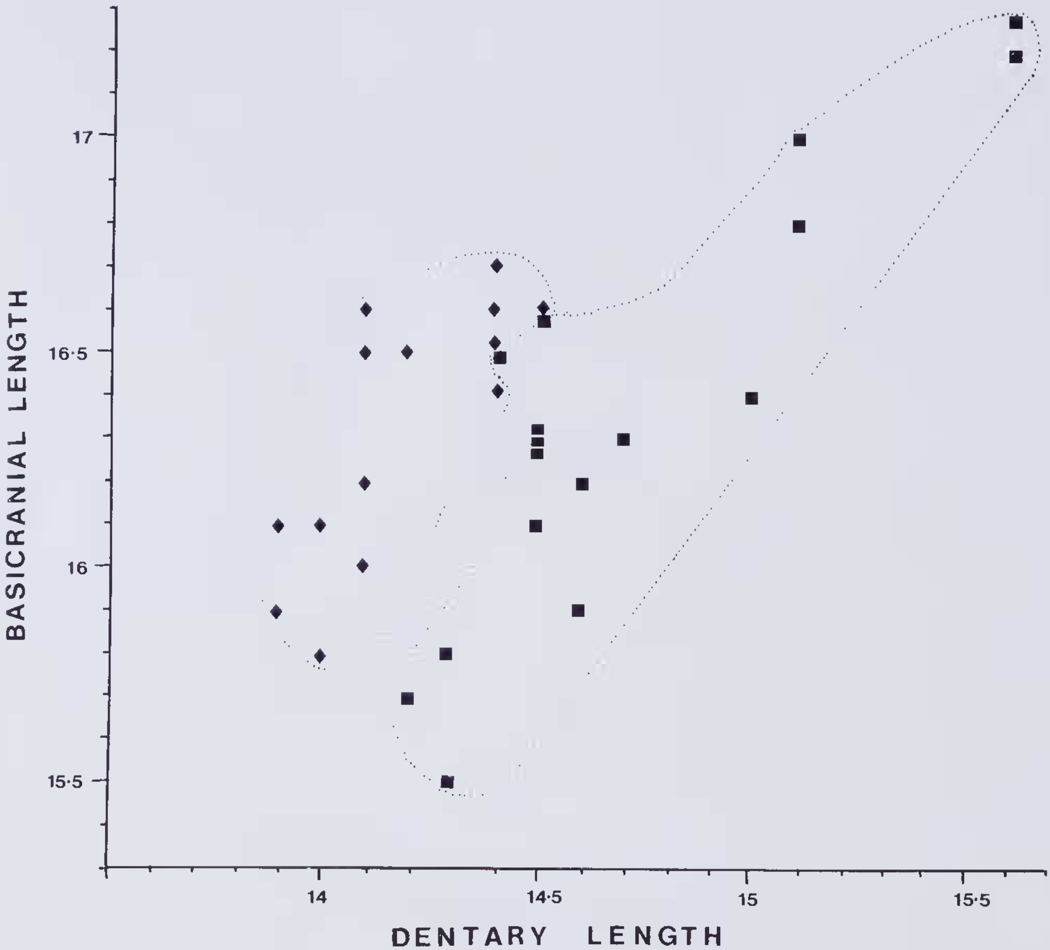


Figure 2 Relationship between the basicranial length and dentary length of *Falsistrellus tasmaniensis* (♦) and *F. mckenziei* (■).

anterolingual cingular cusp variably present on P^4; one to five moderate to large lingual cingular cusps variably present on C^1.

Lower incisors imbricate, trilobed, similar in height but surface area $I_3 > I_2 > I_1$; P_2 half or less than half height P_4, crown area less than half P_4; P_4 three-quarters height C_1; protoconid and hypoconid decrease in height M_{1-3}; M_{1-3} metaconid and entoconid subequal in height, paraconid shorter; hypoconulid M_3 tiny; moderate buccal cingula on all lower teeth except I_{1-2}; lingual cingula absent M_{1-3} except for occasional traces in region between paraconid and metaconid; P_{2-4} encircled with moderate cingula with small anterior and posterior cingular cusplets; C_1 almost encircled with cingula except no immediate anterior cingula, lingual cingula well developed terminating at about one-third height of C_1 in a small anterolingual cusplet; coronoid process of dentary triangular, erect with slightly rounded apex.

External Morphology (mean and range)

Robust, large: snout to anus length 62.3 (57.0-66.3), tail length 47.0 (40.4-51.2), tibia length 21.9 (20.4-23.5), ears moderate length 17.0 (13.5-19.1); ear triangular with rounded apex recurved posteriorly; tragus more than half length of ear 9.4 (8.0-10.5), moderately broad at base with moderate semicircular posterobasal lobe narrowing gently to slightly rounded apex, anterior edge slightly concave, posterior edge moderately convex; line of supratragus projects laterally to meet tragus at its approximate mid point; antitragus small, low, thick lobes; plagiopatagium joins pes at lateral base of fifth digit; calcar approximately two-thirds length of uropatagium posterior margin; calcaneal lobe slight and little elevated; pes moderately large 10.1 (8.2-11.9).

Pelage and Skin

Described from 'puppet' skins. Dorsum uniform Cinnamon Brown from tips of hairs — the basal four-fifths of which are Mummy Brown, interspersed with occasional white hairs. Lateral face and chin sparsely furred, coloured by Warm Buff of skin and Pale Ochraceous Buff and Cinnamon Brown hairs. Ventral surface Light Drab from tips of hairs; in chest and upper abdomen central half of hairs Fuscous, this darker central half of hairs Drab in lower abdomen and Light Drab near vent. Patagia, snout, lips, forearm and feet Fuscous Black; ears Chaetura Drab. Both ventral plagiopatagium and uropatagium lightly furred with Light Drab, in rows along patagial veins next to radius and upper part of uropatagium, denser and less patterned on plagiopatagium beneath humerus.

Glans Penis

Penis length 7.0 (6.6-7.5); head of glans with relatively narrow lateral wings and generally low dorsal hump; urethral groove Y shaped with ventral part of groove traversing length of elongated low ventral mound which covers most of head; skin of head as overlapping thin layers, frequently serrated; preputial skin attached at base of head (Figure 5a).

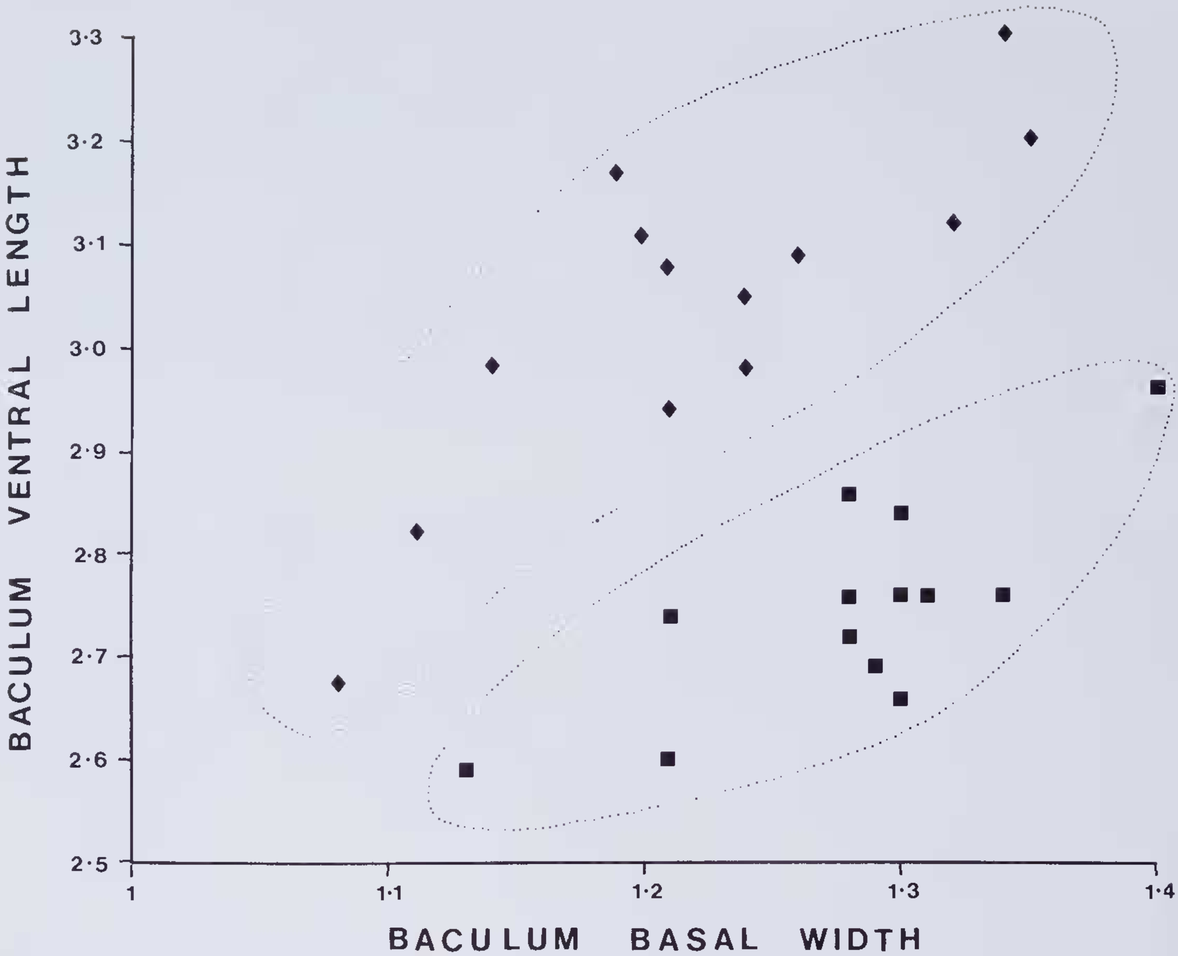


Figure 3 Relationship between length and basal width of baculum of *Falsistrellus tasmaniensis* (♦) and *F. mackenziei* (■).

Baculum

Short 3.04 (2.68-3.33); base broad 1.22 (1.08-1.35); gently tapering to blunt tip with moderate vertical ventral flanges forming a deep groove along its length, particularly basally; base traversed with moderately high dorsal ridge without medial notch, not projecting behind ventral posterior edge of base (Figure 6a). Relationship between overall length (L) and basal width (W) is $L = 1.63\ W + 1.05$ ($r = .83$, $N = 13$, $p < .01$).

Distribution

Sclerophyll forest of Great Divide and towards coast of southeast Queensland, New South Wales and Victoria, and Tasmania (Figure 7).

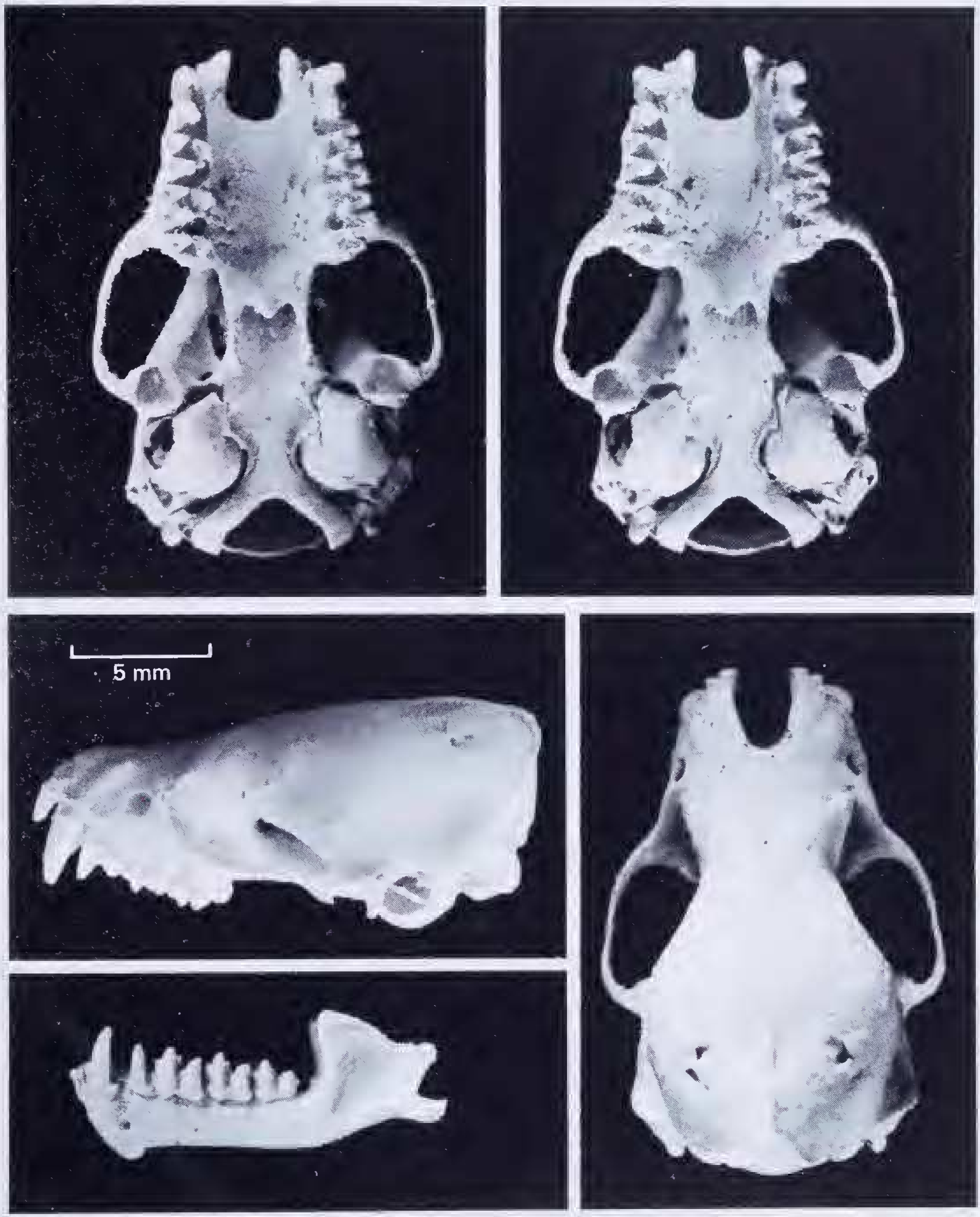
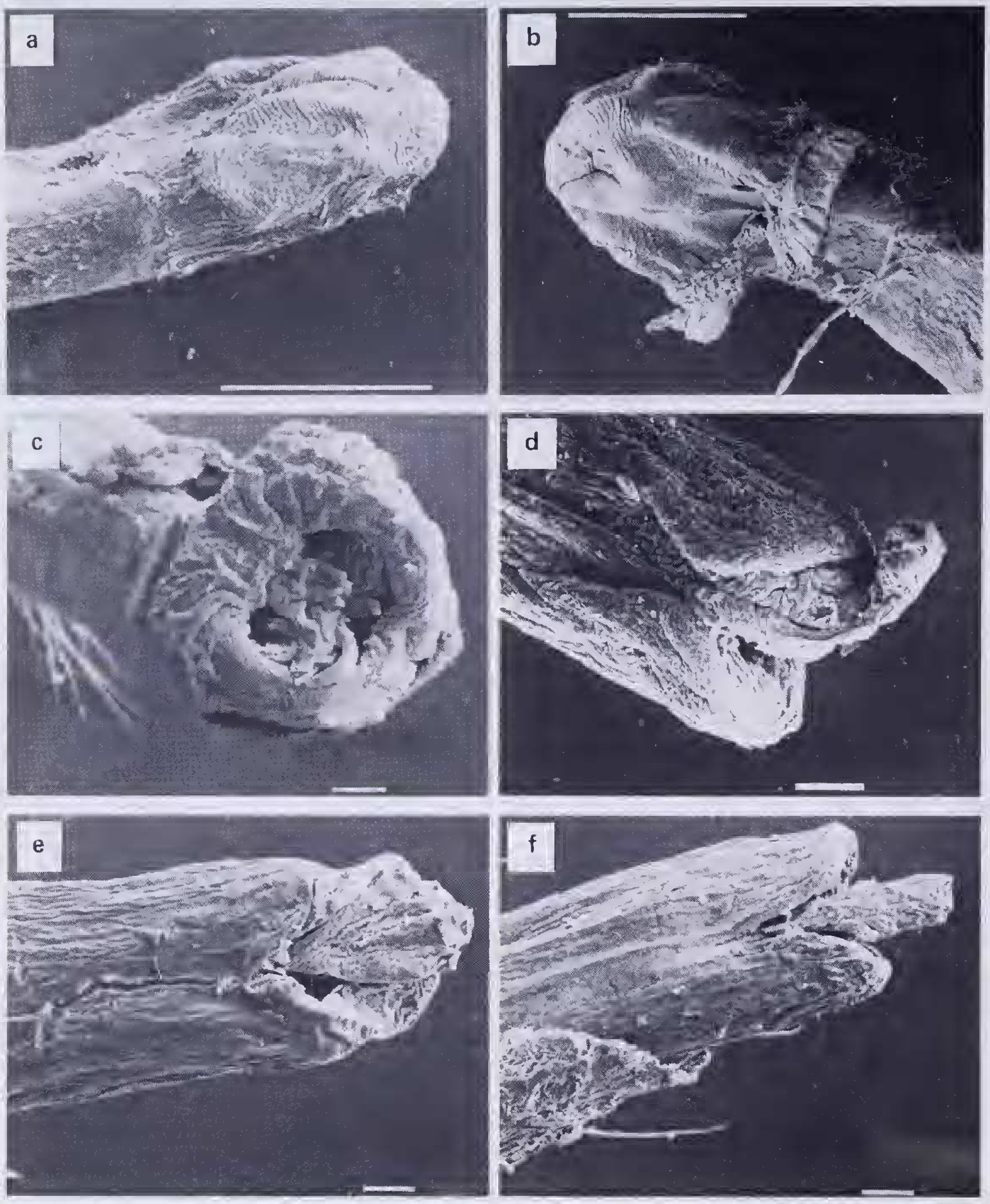


Figure 4 Skull and dentary of *Falsistrellus tasmaniensis* (WAM M16582). Ventral view of skull as stereopairs.


a
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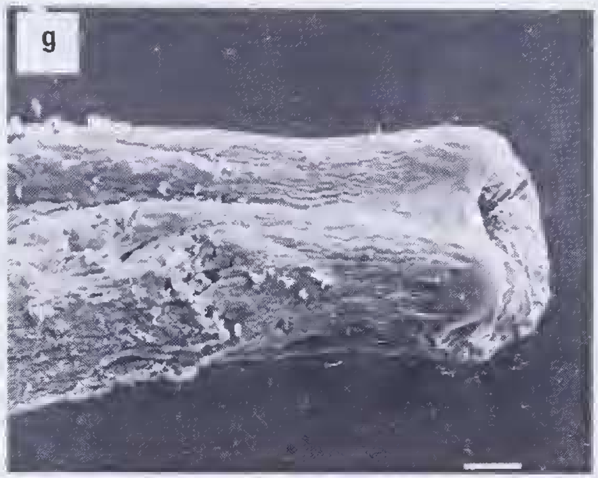

Figure 5 Oblique view of head of glans penis of (a) *Falsistrellus tasmaniensis* (WAM M16585), (b) *F. mackenziei* (WAM M13001), (c) *Pipistrellus westralis* (WAM M23170), (d) *P. adamsi* (EBU C18), (e) *P. papuanus* (AM 4179), (f) *P. wattsi* (AM 3815) and (g) *P. angulatus* (AM 10089). Scale line for *Falsistrellus*, 1000 μm and for *Pipistrellus*, 100 μm.

Specimens Examined

Victoria: Daylesford (37°21′S, 144°09′E), 3 ♀ 2 ♂, C11488-89, C16009, C16011, C16151; Dargo High Plains (37°06′S, 147°09′E), 2 ♂, C16131, C17964; East Gippsland, 5 ♀ 3 ♂, C25960-64, C25909, C35932-33; Elmhurst (37°11′S, 143°21′E), 2 ♂, C16376-77; Glenelg R., 2 ♀ 1 ♂, C24300-02; Highbrow Hill (37°37′S, 145°23′E), 1 ♂, C22306; Hill End (38°00′S, 146°09′E), 1 ♂, C25325; Maroondah Reservoir (37°38′S, 145°34′E), 1 ♂, C22224; Mitta R. (36°33′S, 147°37′E), 1 ♀, C14845; Mt Avoca (37°06′S, 143°21′E), 1 ♀ 2 ♂, C16357-59; Mt Canterbury (37°13′S, 149°12′E), 1 ♂, C24151; Mt Delusion (37°19′S, 147°32′E), 1 ♀ 2 ♂, C17938-39, C17943; Swifts Ck (37°48′S, 146°19′E), 2 ♂, C17954, C17959.

New South Wales: Mt Tinderry (35°42′S, 149°16′E), 4 ♀ 1 ♂, CM2306-09, CM2233; Kosciusko NP. (36°02′S, 148°32′E), 1 ♂, CM6220.

Queensland: Emu-vale (28°14′S, 152°15′E), 1 ♂, JM13300; Killarney (28°19′S, 152°17′E), 1 ♀ 1 ♂, JM13301-02.

Tasmania: 'Tasmania' 2 ♀ 2 ♂, A572/1-572/4 and 1? sex, BM43.2.22.6 (holotype); Ferntree (42°55′S, 147°16′E), 1 ♂, AB1/15670; Hobart (42°53′S, 147°19′E), 1 ♀ 3 ♂, A109, A382, A434, A495; Launceston (41°27′S, 147°10′E), 2 ♀, QVM 1962/1/71, QVM 1980/1/427; Plenty (42°44′S, 146°56′E), 3 ♂, WAM M16582, WAM M16584-85.

Falsistrellus mackenziei sp. nov.

Figures 2, 3, 5b, 6b, 7, 8, 17; Tables 1 and 2

Holotype

WAM M5149, adult male, body in alcohol and skull separate, from Donelly (34° 06′S, 115° 58′E), collected by W. Boswell, 3 August 1962.

Paratypes

Listed in Specimens Examined.

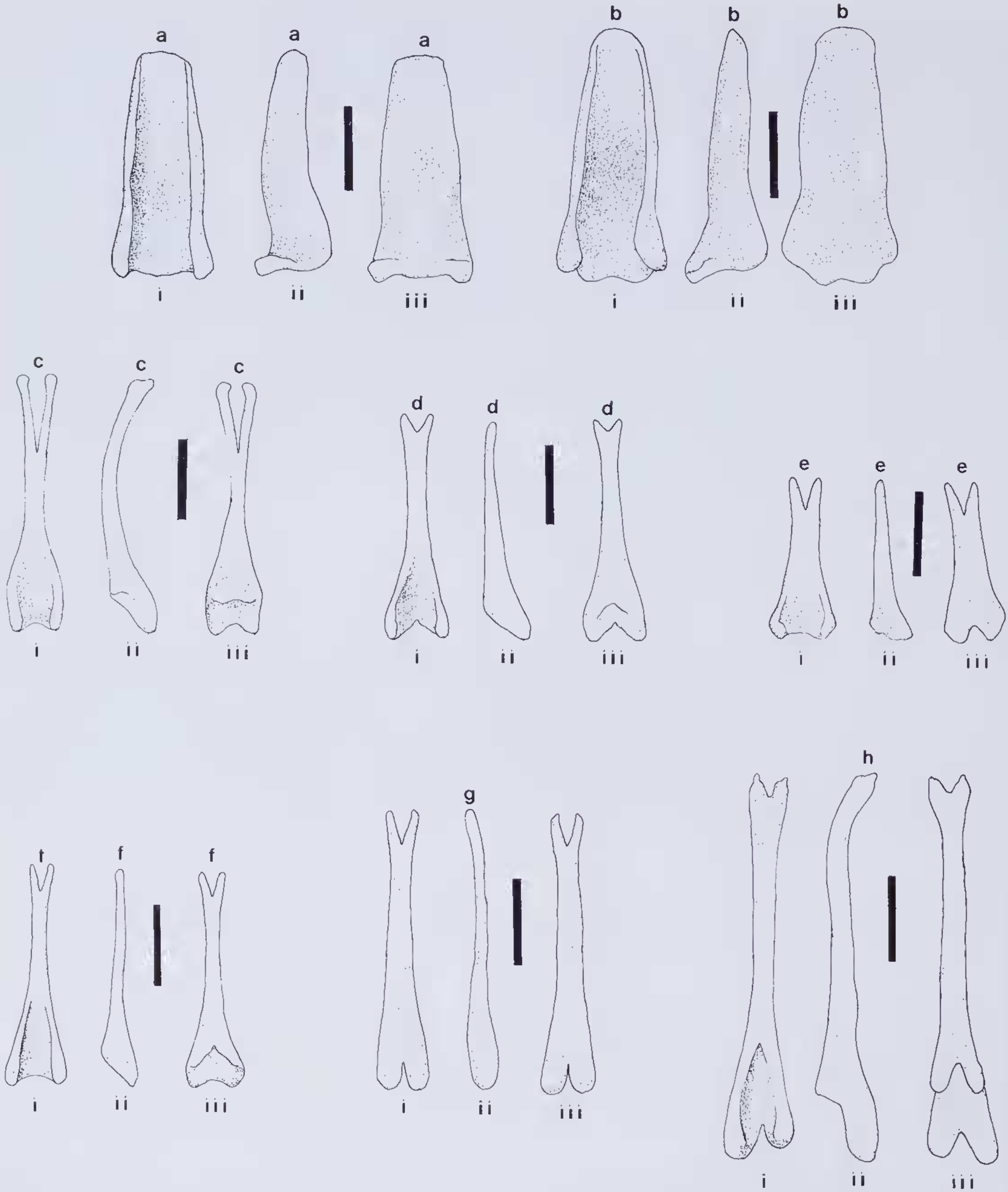

Figure 6 Baculum of (a) *Falsistrellus tasmaniensis* (WAM M16582), (b) *F. mackenziei* (WAM M21074), (c) *Pipistrellus westralis* (WAM M23177), (d) *P. adamsi* (EBU C19), (e) *P. papuanus* (SAM M2838), (f) *P. wattsi* (CM 1957), (g) *P. angulatus* (C 7482) and (h) *P. collinus* (CM 1638). Ventral (i), lateral (ii) and dorsal (iii) view. Scale lines are 1.0 mm.

Figure 7 Distribution of specimens used in this study. *Falsistrellus tasmaniensis* (♦), *F. mackenziei* (■), *Pipistrellus westralis* (○), *P. adamsi* (□), *P. papuanus* (◇), *P. wattsi* (△), *P. angulatus* (▽) and *P. collinus* (∅).

Diagnosis

Differs from *F. tasmaniensis* by being generally larger: greatest skull length (19.2 v. 18.3), zygomatic width (13.2 v. 12.4), braincase width (9.1 v. 8.8), mastoid width (10.5 v. 10.3), palatal length (9.2 v. 8.9), digit III, phalanx I (20.2 v. 18.8); dentary longer relative to basicranial length (Figure 2); glans penis generally both slightly larger and with dorsal hump and lateral wings enlarged; baculum shorter for any given basal width (Figure 3), with notched dorsal basal ridge. Specimens not distinguished on the above may be allocated by using the discriminant functions detailed later.

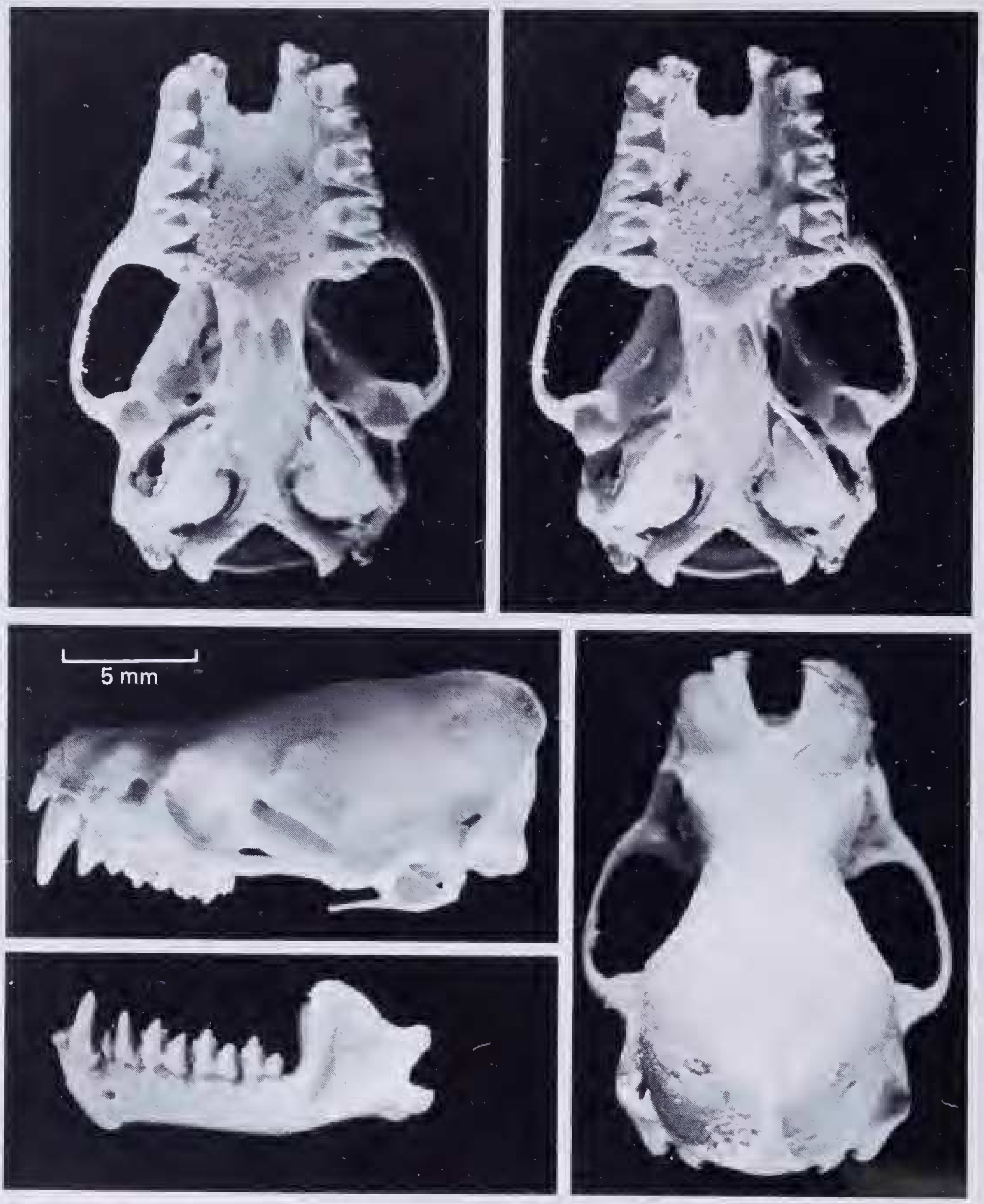

Figure 8 Skull and dentary of *Falsistrellus mackenziei* (WAM M5149, holotype). Ventral view of skull as stereopairs.

Description (mean and range)

Skull and Dentary (Figure 8)

Large robust skull; greatest skull length 19.2 (18.2-20.1); zygomatic width 13.2 (12.2-13.9); interorbital width 5.0 (4.6-5.2); braincase width 9.1 (8.5-9.6); mastoid width 10.5 (9.4-11.0); supraorbital tubercles small to moderate; infraorbital foramen small to moderate separated from orbit by moderate lachrymal bar; bulla length moderate 3.7 (3.3-4.0); P^4 buccal edge moderately notched. Other characters as for *F. tasmaniensis*.

External Morphology

General shape of body, ears, tragus, calcar and lobe, as for *F. tasmaniensis;* snout to anus length 61.7 (55.4-66.6); tail length 46.2 (40.1-53.2); tibia length 22.1 (20.2-23.6); ear length 16.7 (14.0-18.3); tragus length 9.2 (7.7-10.6) and pes length 10.2 (8.2-11.6).

Pelage and Skin

Described from 'puppet' skins. Colour and furring similar to *F. tasmaniensis* but with slightly more rusty hue such that dorsum frequently Dresden Brown rather than Cinnamon Brown with base of hairs Prout's Brown. Ventral surface Light Pinkish Cinnamon, base Sepia. Hairs on ventral patagia Light Pinkish Cinnamon.

Glans Penis

Penis length 7.0 (6.6-7.5); head of glans with broad lateral flanges and high domed dorsal and ventral mounds; urethral grooves Y shaped; skin on head overlapping thin layers, increasingly serrated towards base of head; preputial skin attached at base of head (Figure 5b).

Baculum

Short 2.75 (2.59-2.96); base broad 1.28 (1.13-1.40); shape as for *F. tasmaniensis* except that dorsal basal transverse ridge notched at centre; ridge projecting behind ventral posterior edge of base (Figure 6b). Relationship between overall length (L) and basal width (W). $L = 1.16 W + 1.26$ ($r = .75$, $N = 13$, $p < .01$).

Distribution

Eucalypt forests and woodlands of southwestern Western Australia, does not intrude into the more inland or northern Wheat Belt country (Figure 7).

Etymology

Named after Norman Leslie McKenzie, Department of Fisheries and Wildlife, Western Australia.

Specimens Examined

Western Australia: Boddington (32°55′30″S, 116°26′00″E), 1♀, WAM M19169; Boranup (34°09′S, 115°02′E), 1♂, WAM M4059; Boranup (34°08′S, 115°02′E), 1♀2♂, WAM M4182, WAM M9890-91; Cambray (33°53′S, 115°40′E), 1♀1♂, WAM M12481-82; Carey Brook (34°26′S, 115°58′E), 1♀, WAM M7444; Collie (33°53′S, 116°09′E), 1♂, WAM M11966; Contine (32°52′S, 116°58′E), 1♀, WAM

M7446; Donelly (34°06′S, 115°58′E), 4 ♂, WAM M5149 (holotype), WAM M6328, WAM M6360, WAM M21074; Dwellingup (32°43′S, 116°04′E), 4 ♀, WAM M7770-73; Harvey (33°07′S, 116°02′E), 1 ♂, WAM M8109; Kent R. (34°45′S, 117°03′E), 1 ♀, WAM M11352; Manjimup (34°08′20″S, 116°38′20″E), 1 ♀, WAM M19847; Manjimup (34°08′20″S, 116°38′00″E), 2 ♀, WAM M24335-36; Mt Lindesay (34°52′00″S, 117°27′30″E), 2 ♀, WAM M18594-95; Mt Mitchell (34°46′S, 116°48′E), 1 ♂, WAM M18178; Mt Saddleback (32°54′30″S, 116°28′00″E), 1 ♀, WAM M18840; Nannup (33°59′00″S, 115°38′30″E), 2 ♂, WAM M7443, WAM M7447; Nannup (33°58′30″S, 115°39′00″E), 1 ♂, WAM M19394; Nornalup (34°59′S, 116°51′E), 1 ♀, WAM M24084; Perup R. (34°11′30″S, 116°38′00″E), 2 ♀, WAM M9967-68; Silver Mount (34°34′S, 115°48′E), 1 ♀ 5 ♂, WAM M12996-98, WAM M13001-03; Walpole (34°50′S, 116°33′E), 1 ♀, WAM M12636; Walpole (34°56′S, 116°33′E), 1 ♂, WAM M13004; Wandering (32°07′S, 116°54′E), 1 ♀, WAM M7825; Wheatley (34°07′S, 115°58′E), 3 ♂, WAM M5456-58; Yarloop Siding (32°57′40″S, 115°43′30″E), 8 ♀, WAM M14442-49; York (31°53′S, 116°46′E), 1 ♂, WAM M10143.

Pipistrellus Kaup, 1829

Pipistrellus westralis Koopman, 1984

Figures 5c, 6c, 7, 9, 10, 18; Tables 1 and 3

Pipistrellus tenuis westralis Koopman, 1984: Am. Mus. Novit. 2778: 13-14.

Holotype

Adult male, body in alcohol and skull separate, AMNH 216135 (now lodged in the Western Australian Museum, WAM M22474), from Cape Bossut, Western Australia (*c.* 18°40′S, 121°30′E), collected by G.J. Nelson, W.H. Butler and D.E. Rosen, 15-16 April 1969.

Diagnosis (mean values)

Differs from *P. tenuis (sensu stricto)* in that relative to palatal length the least interorbital distance wider (0.71 v. 0.64); depression of frontals more pronounced; anterior narial emargination longer and more acute; anteropalatal emargination much larger and slightly squarer; P^2 considerably more robust; posterior palate considerably less elevated above sphenoid, lateral and ventral bones surrounding posterior nares not markedly inflated as in *P. tenuis;* outline of posterior nares very much smaller, elongate rather than subcircular; posterior internarial septum wider, vertical rather than sloping such that base of septum and cranial inflection of passage of nares not visible behind postpalatal emargination when viewed vertically; postpalatal spine smaller; sphenorbital sinus projects anterior to posteropalatal margin rather than terminating level with or slightly behind it.

Differs from *P. adamsi* in that skull, dentary and teeth are smaller in nearly all characters: greatest skull length (11.4 v. 12.0), rostrum length (4.7 v. 5.4), mastoid width (6.7 v. 7.1), C^1-M^3 (3.9 v. 4.4), RM^3-LM^3 (5.0 v. 5.5), dentary length (8.0 v. 8.9); upper canines much shorter; skull with more inflated parietal region and more concave interparietal region; posterior palate wider relative to palatal length (0.31 v. 0.27); posteropalatal margin lower (closer to sphenoid), such that posterior nares are distinctly

Table 3: Standardised and unstandardised (in brackets) canonical variates from *P. westralis*, *P. adamsi*, *P. papuanus*, *P. wattsi* and *P. angulatus* for skull and external measurements with sexes combined (see Figure 1 for code to characters). Canonical variate scores are calculated as for Table 2.

CHARACTER	Variate I	Variate II	Variate III
GL	-1.273 (-4.863)	-1.390 (-5.310)	0.932 (3.558)
AOB	-0.114 (-0.803)	0.047 (0.329)	-0.172 (-1.207)
LOW	0.267 (1.944)	0.724 (5.264)	-0.751 (-5.460)
ROL	-0.077 (-0.355)	0.926 (4.245)	-0.229 (-1.049)
MW	-0.447 (-2.229)	0.123 (0.615)	-0.073 (-0.367)
BW	0.812 (5.208)	-1.288 (-8.256)	0.317 (2.030)
CH	-0.097 (-0.699)	0.360 (2.584)	0.033 (0.240)
PL	0.836 (4.619)	-0.726 (-4.009)	-0.910 (-5.028)
PPW	-0.938(-10.624)	0.176 (1.994)	-0.092 (-1.044)
BL	-0.257 (-0.997)	0.407 (1.579)	-0.042 (-0.164)
BUL	0.333 (3.118)	-0.224 (-2.095)	-0.010 (-0.089)
BB	-0.229 (-1.901)	0.675 (5.605)	0.428 (3.553)
OB	0.467 (3.145)	0.138 (0.930)	-0.439 (-2.955)
CW	0.288 (5.155)	-0.099 (-1.774)	0.563 (10.079)
RC^1-LC^1	0.200 (1.423)	0.865 (6.149)	0.447 (3.176)
C^1-M^3	1.548 (12.381)	-0.937 (-7.495)	0.600 (4.802)
M^1-M^3	-0.958(-11.415)	0.583 (6.949)	-0.135 (-1.605)
M^2L	0.129 (2.745)	0.382 (8.120)	0.259 (5.505)
M^2W	-0.077 (-1.206)	0.026 (0.408)	-0.339 (-5.294)
M^3W	-0.042 (-0.620)	0.300 (4.390)	0.373 (5.457)
RM^3-LM^3	-0.736 (-4.796)	0.294 (1.916)	0.012 (0.076)
LR	0.613 (3.993)	-0.380 (-2.475)	-0.303 (-1.973)
RC	-0.530 (-4.967)	0.575 (5.389)	0.246 (2.300)
DL	0.403 (1.948)	1.229 (5.943)	-0.148 (-0.713)
HV	-0.677 (-0.311)	-0.440 (-0.202)	0.190 (0.087)
TV	-0.771 (-0.351)	-0.135 (-0.063)	-0.032 (-0.015)
EL	0.193 (0.263)	-0.441 (-0.599)	0.562 (0.764)
EW	0.463 (0.859)	-0.061 (-0.114)	-0.930 (-1.724)
TL	0.319 (0.731)	-0.029 (-0.067)	-0.132 (-0.302)
RL	0.339 (0.362)	-0.156 (-0.166)	0.507 (0.541)
MCIII	0.371 (0.332)	0.060 (0.054)	0.178 (0.160)
PI	-0.134 (-0.242)	-0.025 (-0.046)	-1.300 (-2.345)
PII	-0.023 (-0.037)	0.509 (0.792)	0.771 (1.198)
PIII	-0.420 (-0.662)	-0.107 (-0.169)	-0.196 (-0.309)
TIB	0.001 (0.002)	-0.588 (-1.058)	0.164 (0.295)
PL	0.528 (1.368)	0.186 (0.482)	0.146 (0.377)
CONSTANT	-23.972	-7.254	-15.771

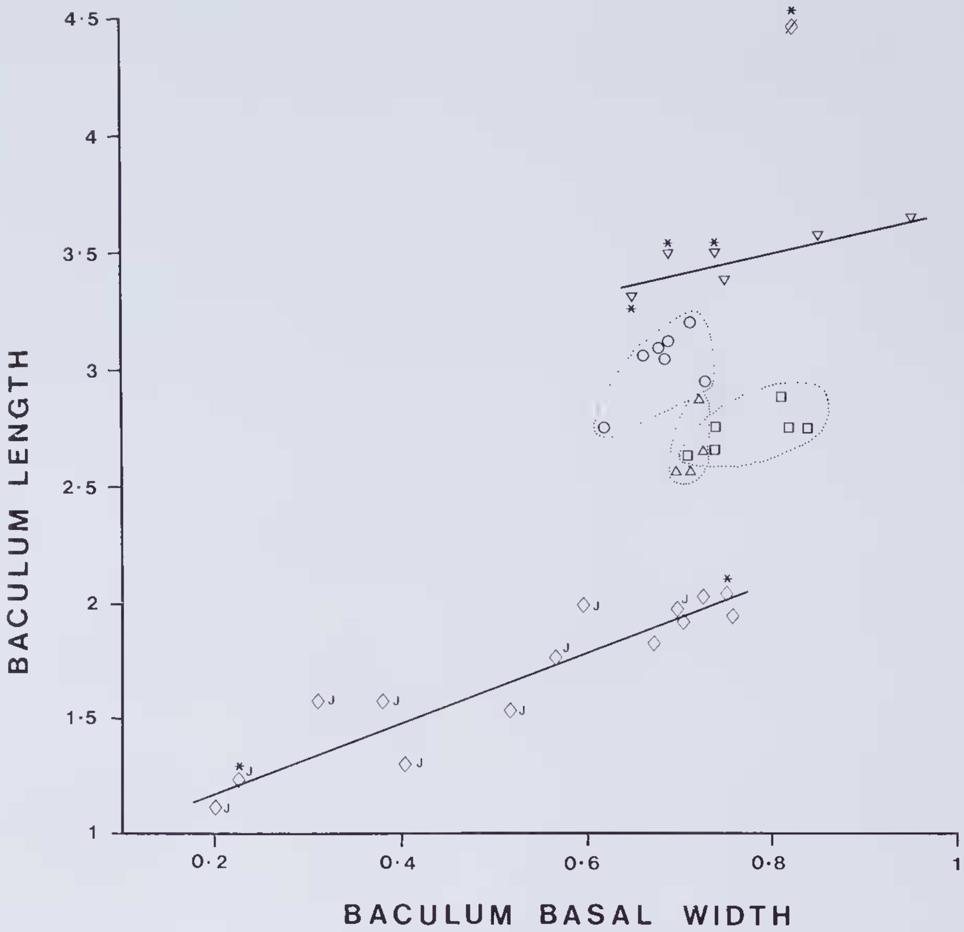

Figure 9 Relationship between baculum length and baculum basal width of *Pipistrellus westralis* (○), *P. adamsi* (□), *P. papuanus* (◇), *P. wattsi* (△), *P. angulatus* (▽) and *P. collinus* (⊘). Regression lines drawn for significant correlations (see text for equations and r values). J, Juveniles; *, specimens used by McKean and Price (1978), remeasured.

oval to elongate rather than subcircular in outline; wider septum separating posterior nares; sphenorbital sinus large, elongate, extends anterior to posteropalatal margin rather than terminating level with or posterior to this margin; radius length (28.9 v. 31.0); ear less rounded at apex; tragus with smaller basal lobe, posterior edge less convex; glans penis with small distal fleshy spines rather than a single fleshy tongue; baculum longer (3.02 v. 2.74) with narrower base (0.68 v. 0.78) (Figure 9), lateral profile of shaft considerably curved rather than straight, distal bifurcating prongs 30% rather than 10% of baculum length.

Differs from *P. papuanus* in that the skull, dentary and teeth are smaller for most characters: greatest skull length (v. 11.9), rostrum length (v. 5.1), mastoid width (v. 7.0), C^1-M^3 length (v. 4.1), RM^3-LM^3 (v. 5.4), dentary length (v. 8.4); posterior margin of palate

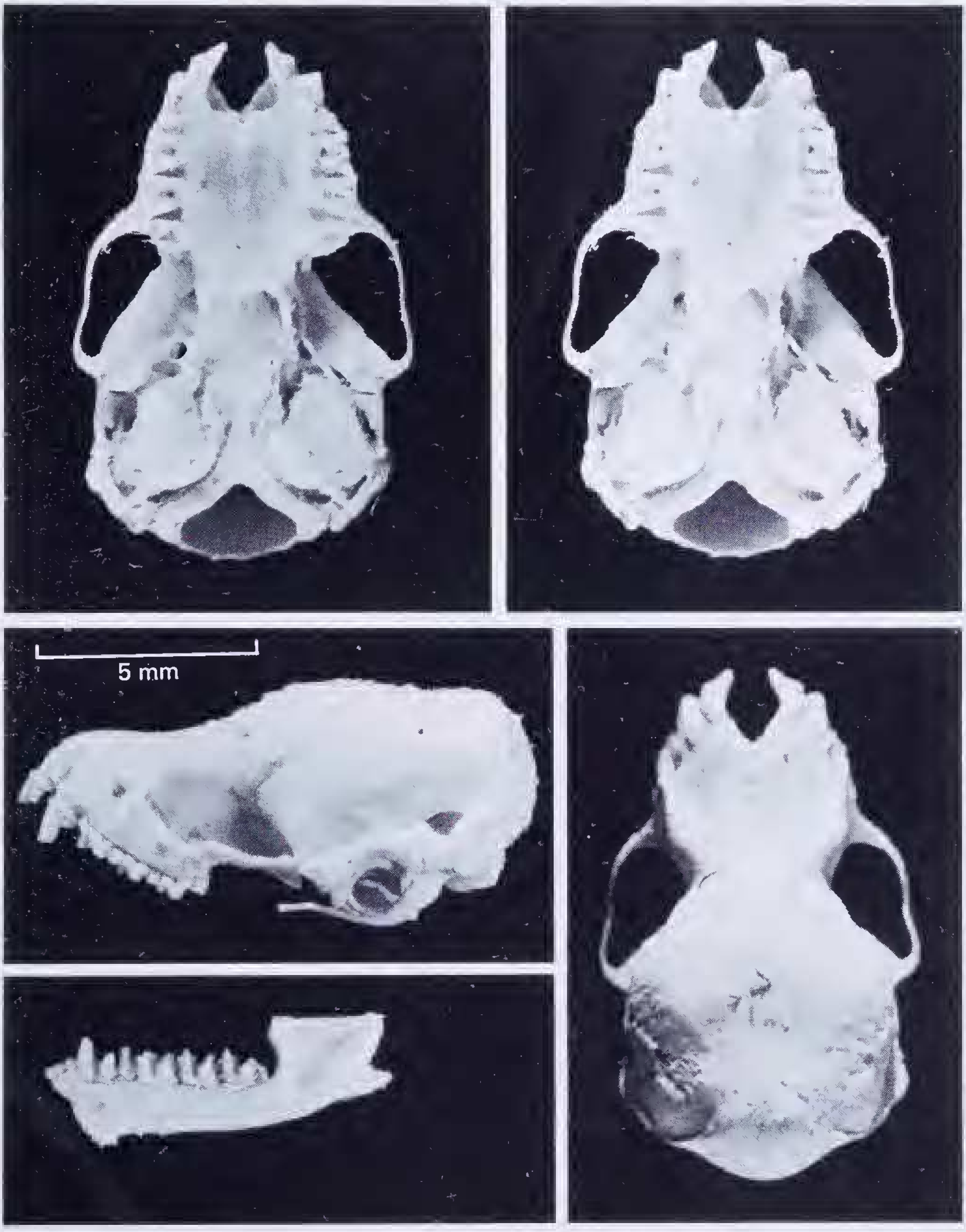

Figure 10 Skull and dentary of *Pipistrellus westralis* (WAM M23172). Ventral view of skull as stereopairs.

lower, such that outline of posterior nares more elongate; sphenorbital sinus elongate, extends anterior to posteropalatal margin rather than terminating level or posterior to this margin; tail longer relative to snout to anus length (0.85 v. 0.73); ears less rounded at apex; tragus posterior edge less convex; glans penis with small distal fleshy spines rather than a single distal fleshy tongue; baculum much longer (v. 1.97), base narrower (v. 0.72) (Figure 9), lateral profile of shaft considerably curved rather than straight, distal bifurcating prongs 30% rather than 10% of baculum length.

Differs from *P. wattsi* in that skull, dentary and teeth are smaller for most characters: greatest skull length (v. 11.6), mastoid width (v. 7.1), C^1-M^3 length (v. 4.1); wider posterior palate (1.6 v. 1.3); rostrum narrower, as indicated by width of RC^1-LC^1 and anteorbital distances relative to rostrum length (0.77 v. 0.82, 0.77 v. 0.82, respectively); postpalatal spine shorter and more slender; posterior margin of palate lower such that posterior nares elongate in outline rather than subcircular; sphenorbital sinus extends anterior to posteropalatal margin rather than terminating level with, or posterior to this margin; shorter radius length (v. 30.9); ears less rounded at apex; tragus posterior edge less convex; glans penis with distal fleshy spines rather than a single distal fleshy tongue; baculum longer (v. 2.67), narrower base (v. 0.72) (Figure 9), lateral profile of shaft considerably curved rather than straight, distal bifurcating prongs 30% rather than 10% of baculum length.

Differs from *P. angulatus* in that skull, dentary and teeth are smaller in most characters: greatest skull length (v. 12.2), mastoid width (v. 6.9), C^1-M^3 (v. 4.3), RM^3-LM^3 (v. 5.2), dentary length (v. 8.5); the shape of the skull differs in that the face is much less concave and relative to greatest skull length has a wider braincase (0.54 v. 0.52), wider mastoid (0.59 v. 0.57), greater least interorbital width (0.32 v. 0.28); longer bulla (0.23 v. 0.21); rostrum broader as indicated by the width of RC^1-LC^1 and anteorbital distances relative to rostrum length (v. 0.73 and v. 0.71, respectively); postpalatal width wider (v. 1.4); sphenorbital sinus extends anterior to margin of postpalatal notch rather than terminating level with or posterior to this notch; radius shorter (v. 32.8); ear shorter (10.0 v. 11.2); tibia shorter (11.9 v. 13.5); ear without prominent concave posterior edge; glans penis with distal fleshy spines rather than a low distal central lobe; baculum shorter (v. 3.48), narrower base (v. 0.77) (Figure 9), lateral profile of shaft considerably more curved and distal bifurcating prongs 30% rather than 10% of baculum length.

Differs from *P. collinus* in that skull, teeth and dentary, and external measurements, with exception of postpalatal width are all shorter: greatest skull length (v. 13.2), mastoid width (v. 7.5), C^1-M^3 (v. 4.7), RM^3-LM^3 (v. 5.8); posterior palate considerably wider relative to palatal length (v. 0.27); rostrum narrower as indicated by width of RC^1-LC^1 relative to rostrum length (v. 0.79); face of skull much less concave; sphenorbital sinus extends anterior to posteropalatal margin rather than terminating level with this margin; radius shorter (v. 37.2); tibia shorter (v. 15.4); baculum much shorter (v. 4.47), narrower base (v. 0.82) (Figure 9), lateral profile of shaft considerably more curved, distal bifurcating prongs 30% rather than 10% of baculum length, base not as markedly notched.

Differs from *P. javanicus* in that all measurements are much smaller: greatest skull length (v. 13.1), mastoid width (v. 7.5), C^1-M^3 (v. 4.9), dentary length (v. 9.5), radius length

(v. 33.2), tibia length (v. 13.3); least interorbital region broader relative to skull length (0.32 v. 0.28); posterior palate broader relative to palatal length (v. 0.30); lambdoidal and sagittal crest do not meet to form a slight occipital crest as in *P. javanicus;* glans penis with distal fleshy spines rather than a broad distal lobe with short spicules; baculum much shorter (v. > 5mm) with distal prongs 30%, rather than 10% length of shaft.

Differs from *P. imbricatus* in that most measurements are much smaller: greatest skull length (v. 12.4), mastoid width (v. 7.2), C^1-M^3 (v. 4.2), dentary length (v. 8.7), radius length (v. 33.5), tibia length (v. 13.7). However, rostrum longer (v. 4.2) and narrower as indicated by RC^1-LC^1 and anteorbital width relative to rostrum length (v. 1.02 and v. 0.98, respectively); posterior palate wider (v. 1.4) and distance between bullae wider (1.10 v. 0.74); P^2 considerably larger; mesial rostral groove more pronounced; anterior nares arrow-shaped rather than spatulate; mesial edge of cochlea smoothly curved and not angular; postpalatal spine smaller; outline of posterior nares more elongate; baculum shorter (v. > 11), shaft slightly curved and not sinuously shaped, distal prongs 30%, rather than 10% length of shaft.

Description (mean and range)

Skull and Dentary (Figure 10)

Small fragile skull: greatest skull length 11.4 (11.1-11.9), zygomatic width 7.5 (7.3-7.8), interorbital width 3.6 (3.3-3.9), cranial width 6.2 (5.9-6.5), mastoid width 6.7 (6.4-7.0), dentary length 8.0 (7.7-8.2); lateral profile of skull rising moderately behind premaxilla to middle region of parietal, and then almost level to interparietal; moderate median rostral depression; anterior nares narrow arrow-shape, extending approximately to a line joining posterior edge of infraorbital foramen; supraorbital tubercles slight to absent; wide interorbital region, infraorbital foramen small, located above M^1 parastyle; sagittal crest absent; lambdoidal crest weak and only laterally — no occipital crest; zygoma weak; anterior palatal emargination broad, spatulate, reaches posteriorly to centre of P^2; palatal depression moderate; posterior palate wide 1.6 (1.5-1.9) and extends posteriorly such that viewed vertically it covers base of median palatal septum and openings of posterior nares; posterior narial outline oval to elongate; median posterior septum supporting palate moderately wide, short, vertical; postpalatal spine very small and broadly triangular; pterygoid process short, triangular, moderately acute apex, slightly recurved posteriorly; sphenorbital sinus slightly flared laterally, extends anterior of posterior margin of palate; basisphenoid depressions small, shallow; bulla length moderate 2.6 (2.3-2.7), covers two-thirds cochlea; eustachian part varies from short thin spicule to being barely perceptible; glenoid surface for condyle of mandible subcircular or oval and longer than wide; I^1 bicuspid with posterior cusp varying in height from a basal position to about half height of anterior cusp; I^2 four-fifths length I^1, usually slightly shorter than posterior cusp I^1, wider base than I^1, not extruded from tooth row, surface facing C^1 concave; diastema between I^2 and C^1; C^1 posterior cutting edge at a slight to moderate angle to line of tooth row with moderate to absent basal cusplet, base elongate; P^2 surface area subequal to that of I^2, approximately half height P^4, slightly intruded from line of tooth row; paracrista length increases M^{1-3}; metacrista length M^1 less than or subequal to that of M^2; M^3 shape as in *Falsistrellus*; paracone M^{1-2} subequal in height, taller than paracone M^3, shorter than metacone M^{1-2}; metacone M^{1-2} subequal in height; hypocone M^{1-2} poorly developed; protocone well developed; cingula encircling I^{1-2} (weak in antero-lingual area), C^1 and P^{2-4}; anterior cingula M^{1-3} weak or absent; lingual cingula moderately well developed M^{1-3}, absent beneath protocone; posterior cingula moderate M^{1-2}, very slight to absent M^3; anterolingual cingular cusplets large P^4, moderate I^2.

Height I_{1-3} subequal; width $I_1 > I_2 > I_3$; I_3 more robust than I_{1-2}; I_{1-3} trilobed, not imbricate; P_2 large, four-fifths height and subequal to surface area P_4, four times surface area I_3, slightly extruded from line of tooth row; height M_{1-3} paraconid < metaconid < entoconid; M_{1-3} protoconid taller than hypoconid; M_3 hypoconulid small to absent; moderate cingula encircling C_1, P_2 and P_4; moderate anterior and posterior lingual cingular cusplet C_1, P_2 and P_4; moderate anterior, posterior and buccal cingula M_{1-3}; first triangle smaller than second triangle M_{1-3}; coronoid process of mandible with posterior edge much longer than anterior edge, not erect, apex slightly rounded.

External Morphology

Small, delicate: snout to anus length 37.0 (34.4-42.2), tail length 31.5 (29.0-37.2), tibia length 11.9 (11.1-12.6), ear moderate length 10.0 (8.1-11.0), broadly triangular with rounded apex, posterior edge straight, or slightly concave upper half; tragus length 5.0 (4.7-6.1) less than half that of ear, wider at base with small broadly triangular posterior basal lobe, but narrowing only slightly to apex, anterior edge gently concave, posterior edge gently convex; supratragus small, projects laterally to meet tragus approximately two thirds up its length; antitragus lobe moderate height, semicircular, thin; plagiopatagium joins pes at lateral base of fifth digit; calcar approximately two-thirds of uropatagium posterior margin; calcaneal lobe elongate and little elevated; pes small 4.9 (4.4-5.7).

Pelage and Skin

Described from dried alcohol preserved specimens. Shoulders and back Dresden Brown from tips, basal three-quarters Fuscous Black. Forehead and face Buckthorn Brown. Ventral surface Light Ochraceous Buff from tips, basal three-quarters Fuscous Black. Skin of snout, ears, forearm and feet Dresden Brown; patagia Mummy Brown. Uropatagium lightly furred along veins and plagiopatagium unpatterned beneath humerus with Light Ochraceous Buff.

Glans Penis

Penis length 5 (4-6); head of glans slightly flared at distal end with slight ventral and larger dorsal groove on rim; urethral opening subcircular from centre of which project numerous shallow fleshy spines or lobes; shaft of glans a smooth rod; preputial skin attached at about 1.5 mm from distal end (Figure 5c).

Baculum

Relatively long 3.02 (2.76-3.20) (N = 7); base narrow 0.68 (0.62-0.73); shaft narrow, gently curved with last 30% bifurcated (Figure 6c).

Distribution

Coastal and near coastal country, including mangroves of Northern Australia including Kimberley, Western Australia, Northern Territory and eastern part of Gulf of Carpentaria (Figure 7).

Specimens Examined

Northern Territory: Thring Ck (12°14′S, 131°54′E), 2♀, CM4622-23.

Queensland: Karumba (17°29′S, 140°50′E), 1♀1♂, AM M12816-17.

Western Australia: Black Cliff Pt (15°02′30″S, 128°06′00″E), 2♀2♂, WAM (M23062-3, M23177, M23072); Cambridge Gulf (15°11′S, 128°17′E), 4♀6♂, WAM (M23060, M23064-71, M23174); Cape Bossut (18°42′20″S, 121°37′00″E), 1♀1♂, WAM M23175, EBU 118, (*c.*18°40′S, 121°30′E), WAM M22474, 1♂ holotype (= AMNH216135); Dampierland (16°34′15″S, 122°50′50″E), 2♀1♂, WAM M22668-70; Glenelg R. (15°48′S, 124°45′E), 2♀, WAM (M23173, M23061); Pt Torment (17°15′S, 123°44′E), 1♀3♂, WAM (M23170-2, M23176); Prince Regent R. (15°27′S, 125°05′E), 1♀, WAM M23169; Sunday I. (16°25′S, 123°11′E), 1♀, WAM M23168.

Pipistrellus adamsi sp. nov.

Figures 5d, 6d, 7, 9, 11, 18; Tables 1 and 3

Holotype

JM5022, adult male, body in alcohol and skull separate, soft tissue removed for electrophoresis, from 40 km E Archer River Crossing, Cape York, Queensland (13°27′S, 143°18′E), collected by Stanley Flavell on 27 September 1983.

Paratypes

Listed in Specimens Examined.

Diagnosis (mean values)

Differs from *P. tenuis (sensu stricto)* in that it is larger in most measurements: greatest skull length (12.0 v. *c.* 10.9), mastoid width (7.1 v. 6.8), C^1-M^3 (4.4 v. 3.7), dentary length (8.9 v. 7.3), radius length (31.0 v. 26.4), tibia length (12.3 v. 10.4); posterior palate narrower (1.5 v. 1.6) and canine basal width narrower (0.6 v. 0.7); slight extension of sagittal crest forward to supraorbital protuberances absent in *P. tenuis;* anterior narial emargination much larger and less arrow-shaped; P^2 more robust; anterior palatal emargination much larger and squarer; posterior narial opening smaller, lateral and ventral bones surrounding posterior narial passage not markedly inflated as in *P. tenuis;* posterior internarial septum vertical, rather than sloping, such that base of septum and

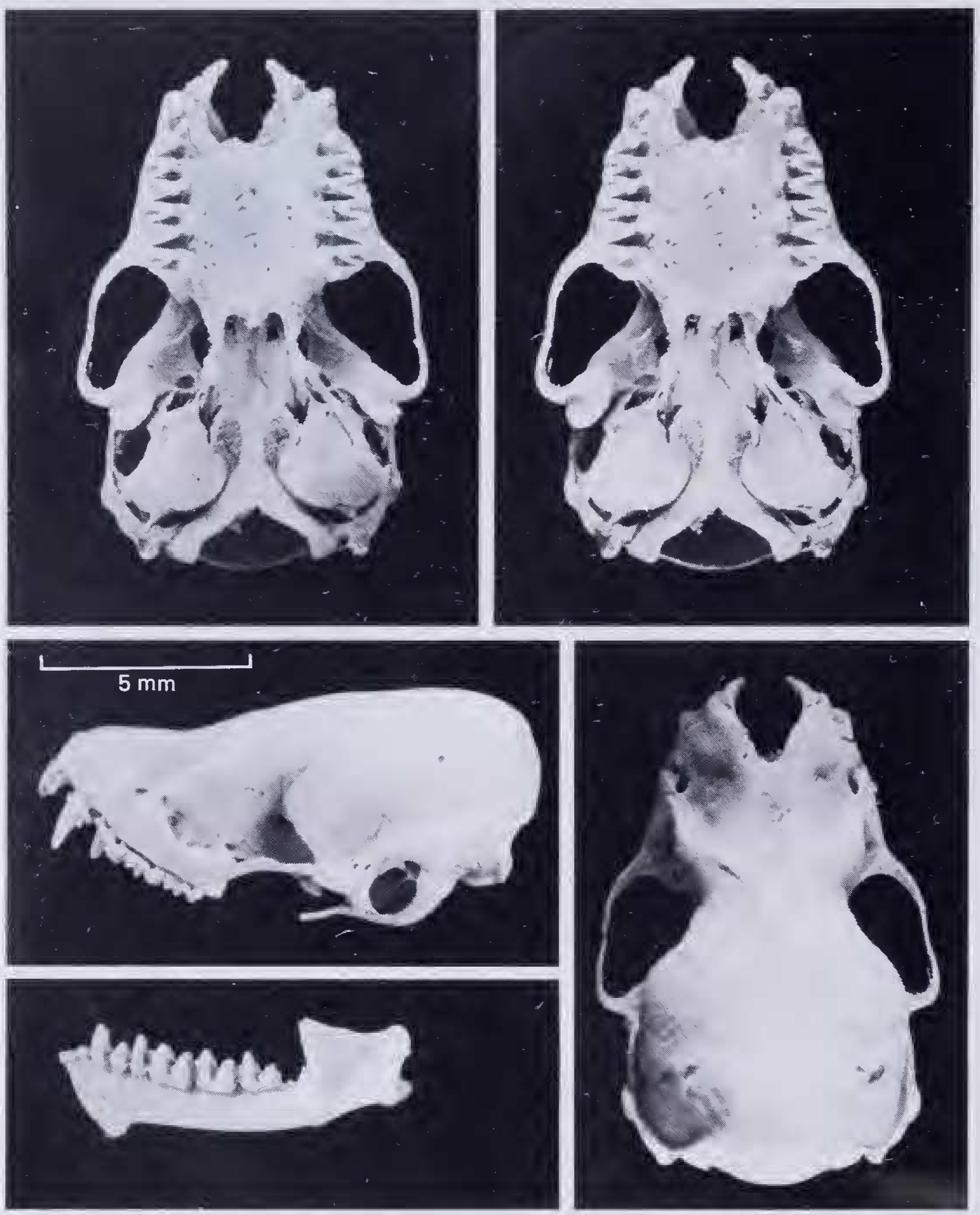

Figure 11 Skull and dentary of *Pipistrellus adamsi* (JM 5022, holotype). Ventral view of skull as stereopairs.

the cranial inflection of narial passage not visible behind posteropalatal margin when viewed vertically; postpalatal spine larger.

Differs from *P. westralis* in that the skull, dentary and teeth are larger in nearly all characters: greatest skull length (v. 11.4), rostrum length (5.4 v. 4.7), mastoid width (v. 6.7), C^1M^3 (v. 3.9), $RM^3 LM^3$ (5.5 v. 5.0), dentary length (v. 8.0); upper canines much longer; skull with less inflated parietal region and less concave interparietal region; posterior palate narrower relative to palatal length (0.27 v. 0.31); posteropalatal margin higher (further from sphenoid), such that posterior nares are subcircular in outline rather than oval to elongate; septum separating posterior nares narrower; sphenorbital sinus terminates level with or posterior to posteropalatal margin rather than anterior to this margin; radius length (v. 28.9); ear more rounded at apex; tragus with larger basal lobe, posterior edge more convex; glans penis with a single distal fleshy tongue rather than small fleshy spines; baculum shorter (2.74 v. 3.02) with broader base (0.78 v. 0.68) (Figure 9), lateral profile of shaft straight rather than considerably curved, distal bifurcating prongs 10% rather than 30% of baculum length.

Differs from *P. papuanus* in that nearly all measurements recorded average larger: greatest skull length (v. 11.9), mastoid width (v. 7.0), C^1-M^3 (v. 4.1), dentary length (v. 8.4); rostrum tends to be longer relative to greatest skull length (0.45 v. 0.43); posterior palate narrower relative to palatal length (v. 0.33); larger anterior palatal emargination; radius length (v. 29.8); baculum considerably longer (v. 1.97), base only slightly wider (v. 0.72) (Figure 9).

Differs from *P. wattsi* in that nearly all measurements recorded average larger: greatest skull length (v. 11.6), C^1-M^3 (v. 4.1), RM^3-LM^3 (v. 5.1), dentary length (v. 8.3); rostrum longer relative to greatest skull length (0.45 v. 0.42) and narrower as indicated by width of RC^1-LC^1 and anteorbital distances relative to rostrum length (0.78 v. 0.82, 0.74 v. 0.82, respectively); braincase width narrower relative to greatest skull length (0.53 v. 0.56); postpalatal spine much smaller.

Differs from *P. angulatus* in that the skull is shorter and broader: greatest skull length (v. 12.2), least interorbital width (3.7 v. 3.4), mastoid width (v. 6.9); rostrum and palate longer relative to greatest skull length (v. 0.42, and 0.47 v. 0.45 respectively); rostrum broader, as indicated by width RC^1-LC^1 and anteorbital distances relative to rostrum length (v. 0.73, v. 0.71, respectively); anteropalatal emargination larger; face of skull much less concave; radius shorter (v. 32.8); tail shorter (30.1 v. 32.1); tibia shorter (v. 13.5); glans penis broader with more prominent distal fleshy lobe; baculum shorter (v. 3.48), base wider relative to its length (0.28 v. 0.22) (Figure 9), shaft narrower.

Differs from *P. collinus* in that most skull, teeth, dentary and external measurements are smaller: greatest skull length (v. 13.2), mastoid width (v. 7.5), C^1-M^3 (v. 4.7), RM^3-LM^3 (v. 5.8), dentary length (v. 9.4); face of skull much less concave and rostrum broader as indicated by width RC^1-LC^1 and anteorbital distance relative to rostrum length (v. 0.79, v. 0.77, respectively); radius shorter (v. 37.2); tibia shorter (v. 15.4); baculum much shorter (v. 4.47), base slightly narrower (v. 0.82) (Figure 9) and not as markedly notched ventrally, shaft straight and not as markedly curved in region of distal prongs.

Differs from *P. javanicus* in that all measurements average smaller: greatest skull length (v. 13.1), mastoid width (v. 7.5), C^1-M^3 (v. 4.9); dentary length (v.9.5), radius length (v. 33.2), tibia length (v. 13.3); lamdoidal and sagittal crest slight to absent in occipital region and do not meet to form slight crest as in *javanicus;* interorbital region wider relative to greatest skull length (0.31 v. 0.28); anterior narial emargination slightly more flared; posterior palate narrower relative to palatal length (v. 0.30); posterior margin of palate lower; sphenorbital sinus more flared laterally and does not terminate anterior to margin of posteropalatal margin; opening of posterior nares subcircular rather than elongate; glans penis with longer and narrower fleshy lobe without short spicules; baculum much shorter (v. > 5.0), lateral profile of shaft straight rather than generally slightly curved.

Differs from *P. imbricatus* in that rostrum longer relative to greatest skull length (v. 0.34); following characters narrower relative to palatal length: least interorbital width (0.66 v. 0.69), anteorbital width (0.71 v. 0.79), RM^3-LM^3 (0.98 v. 1.04), RC^1-LC^1 (0.75 v. 0.83); P^2 considerably larger; anterior nares narrower and more arrow-shaped rather than spatulate; sphenorbital sinus terminates level or posterior to posteropalatal margin rather than anterior to it; posterior palate more elevated above sphenoid; opening of posterior nares less elongate in outline; bulla shorter (2.7 v. 3.0), wider between bullae (1.4 v. 0.7); mesial edge of cochlea smoothly curved and not angular; radius shorter (v. 33.5); tibia shorter (v. 13.7); baculum much shorter (v. > 11.0), shaft straight and not sinuous.

Description (mean and range)

Skull and Dentary (Figure 11)

Small fragile skull: greatest skull length 12.0 (11.7-12.6), zygomatic width 8.1 (8.0-8.2), interorbital width 3.7 (3.6-3.9), mastoid width 7.1 (6.9-7.3), dentary length 8.9 (8.7-9.3). Similar to *P. westralis* in: dorsal profile of skull, rostral depression, infraorbital foramen, lachrymal bar, bulla size and shape, dental cusp and cingular morphology, glenoid surface for mandibular condyle, zygoma, palatal depression, pterygoid process. Supraorbital tubercle small to absent; parietal considerably inflated; sagittal crest absent; lambdoidal crest moderate, decreases towards supraoccipital, absent at apex; mastoid process moderately well developed; anteropalatal emargination wide, spatulate, extends posteriorly to P^2; postpalatal width narrow, high above sphenoid; posterior median septum supporting palate tall and narrow, almost vertical, not visible behind posteropalatal margin when viewed vertically; outline of posterior nares subcircular, large, just visible behind posteropalatal margin when viewed vertically; posterior palate slightly flared dorsolaterally around passage of posterior nares; moderate median presphenoidal groove; usually with a moderate sized rectangular foramen on either side of presphenoid, extending from immediately posterior to opening of posterior nares to level with base of pterygoid process; basisphenoid depression shallow; sphenorbital sinus moderately flared laterally, does not extend anterior to posterior margin of palate, but occasionally level with it; I[1] bicuspid; I[2] usually not reaching posterior cusp I[1], not extruded from line of tooth row; C[1] posterior cutting edge at slight to moderate angle to tooth row, with small to moderate basal cusplet, base elongate; P[2] three-quarters surface area of I[2], less than half height P[4]; metacrista M^{1-2} subequal length. P_2 two-thirds height and four-fifths surface area P_4, four times surface area I_3, slightly extruded from line of tooth row.

External Morphology

Small, delicate: snout to anus length 37.2 (33.9-42.0), tail length 30.1 (26.7-34.6), tibia length 12.3 (10.7-13.1), ear length 11.2 (9.4-12.0); ear broadly rounded; tragus about half length of ear 5.8 (5.2-6.6) with moderate triangular posterior basal lobe, recurved anteriorly, anterior edge gently concave, posterior edge markedly convex such that tragus broadest in middle, apex slightly rounded; supratragus small, projects laterally to meet tragus approximately two-thirds up its length; antitragal lobe moderately high, semicircular, thin; plagiopatagium joins pes at lateral base of fifth digit; calcar approximately two-thirds of uropatagium posterior margin, lobe moderate, semicircular; pes small 5.4 (5.1-5.9).

Pelage and Skin

Described from dried alcohol preserved specimens. Shoulders and back Mummy Brown from tips, basal three-quarters Fuscous. Forehead and face Prouts Brown. Chest and venter Light Drab from tips, basal three-quarters Fuscous Black, around vent Light Drab. Beneath chin Drab. Skin of snout, ears, patagia, forearm and feet Fuscous Black. Uropatagium lightly furred along veins and plagiopatagium unpatterned beneath humerus with Light Drab.

Glans Penis

Penis length 6 (6-7); head of glans slightly flared with small ventral flaps against shaft; dorsal and ventral groove on distal lip surrounding urethral opening; relatively long fleshy lobe projecting from ventral distal edge of glans; shaft relatively long with preputial attachment approximately 1mm from distal end of glans (Figure 5d).

Baculum

Relatively long 2.74 (2.63-2.89)(N = 6); base broad 0.78 (0.71-0.84); shaft narrow, not curved, bifurcated last 10% of length (Figure 6d).

Distribution

Recorded only from central Cape York, Queensland, and near Darwin, Northern Territory (Figure 7).

Etymology

Named after Mark Andrew Adams, Evolutionary Biology Unit, South Australian Museum.

Specimens Examined

Paratypes

Northern Territory: Darwin (12°27′S, 130°50′E), 1♀ ,EBU B161; Reynolds R. (*c.* 13°16′S, 130°41′E), 1♀, EBU B208.

Queensland: 40km E Archer R. Crossing (13°27′S, 143°18′E), 4♂ 2♀, EBU (C12, C14-15, C17-19); Coen (13°57′S, 143°12′E), 3♂ , JM2420, JM2754, JM2484; 20km S Coen (14°02′S, 143°12′E), 3♂ 7♀, EBU (C7, C55-9, C81-2, C107, C110).

Pipistrellus papuanus (Peters and Doria, 1881)

Figures 5e, 6e, 7, 9, 12, 18; Tables 1 and 3

Vesperugo papuanus Peters and Doria, 1881: Ann. Mus. Stor. Nat. Genova. 16: 696.

Vesperugo papuanus orientalis Meyer, 1899: Abh. Ber. K. Zool. Anthrop-Ethn. Mus. Dresden. 7: 14, Bongu, Astrolabe Bay, north New Guinea.

Holotype

MSNG 11660, adult female, body in alcohol and skull separate, from Salawatti, west New Guinea (= Irian Jaya).

Diagnosis (mean values)

Differs from *P. westralis* and *P. adamsi* as detailed in earlier diagnoses.

Differs from *P. tenuis (sensu stricto)* in that it averages slightly larger in most measurements: particularly C^1-M^3 (4.1 v. 3.7), RM^3-LM^3(5.4 v. 4.7), lower tooth row (5.1 v. 4.7),dentary length (8.4 v. 7.3), radius length (29.7 v. 26.4), tibia length (12.0 v. 10.4); anteronarial emargination much larger and less arrow-shaped; frontals more concave; anteropalatal emargination similar shape but much larger extending level to posterior edge of P^2 rather than terminating level to anterior face of P^2; posterior palate not as elevated above sphenoid, posterior internarial septum much shorter, vertical rather than sloping; posteronarial opening much smaller, oval rather than subcircular outline; lateral and ventral bones surrounding posteronarial passage little rather than considerably inflated; P^2 iarger.

Differs from *P. wattsi* in that the posterior palate is broader relative to palatal length (0.33 v. 0.25); rostrum narrower as indicated by width RC^1-LC^1 and anteorbital distance relative to rostrum length (0.78 v. 0.82, 0.73 v. 0.82, respectively); postpalatal spine smaller; anteropalatal emargination smaller; baculum shorter (1.97 v. 2.67), base wider relative to length (0.37 v. 0.27) (Figure 9).

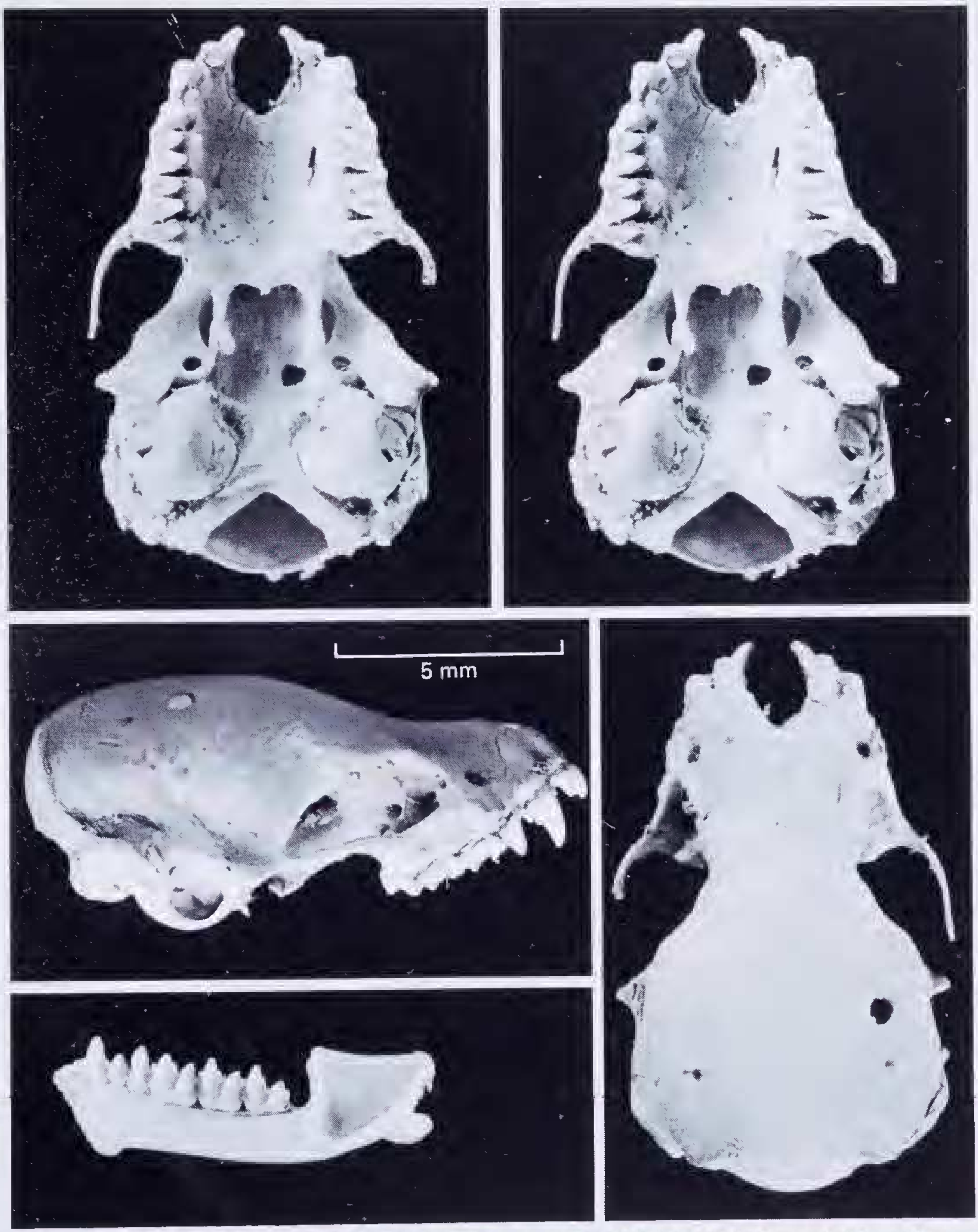

Figure 12 Skull and dentary of *Pipistrellus papuanus* (MSNG 11660, holotype). Ventral view of skull as stereopairs.

Differs from *P. angulatus* in that skull shorter and broader relative to greatest skull length: least interorbital width (0.29 v. 0.28), mastoid width (0.59 v. 0.57), zygomatic width (0.67 v. 0.62); rostrum wider as indicated by width of RC^1-LC^1 and anteorbital width relative to rostrum length (v. 0.73, v. 0.71, respectively); posterior palate wider relative to palatal length (v. 0.25); face of skull much less concave; radius shorter (v. 32.8); tail shorter (28.3 v. 32.1); tibia shorter (v. 13.5); distal end of glans penis broader with more prominent distal fleshy lobe; baculum much shorter (v. 3.48) (Figure 9).

Differs from *P. collinus* in that most skull, dentary, teeth and external measurements are smaller: greatest skull length (11.9 v. 13.2), mastoid width (7.0 v. 7.5), C^1-M^3(v. 4.7), RM^3-LM^3(v. 5.8), dentary length (v. 9.4); posterior palate wider relative to palatal length (v. 0.27); face of skull much less concave and rostrum narrower as indicated by RC^1-LC^1 and anteorbital width relative to rostrum length (v. 0.79, v. 0.77, respectively); radius shorter (v. 37.2); tibia shorter (v. 15.4); baculum much shorter (v. 4.47) and base only slightly narrower (0.72 v. 0.82) (Figure 9) and not as markedly notched ventrally, shaft straight and not markedly curved in region of distal prongs.

Differs from *P. javanicus* in that all measurements are smaller: greatest skull length (v. 13.1), mastoid width (v. 7.5), C^1-M^3 (v. 4.9), dentary length (v. 9.5), radius length (v. 33.2),tibia length (v. 13.3); posterior palate wider relative to palatal length (v. 0.30); sphenorbital sinus more flared laterally and does not extend anterior to posteropalatal margin; lambdoidal crest much weaker in occipital region; glans penis with narrower and longer central distal fleshy lobe without small fleshy spicules; baculum much shorter (v. >5), relatively broader base, shaft flatter in lateral profile.

Differs from *P. imbricatus* in that most measurements are smaller: greatest skull length (v. 12.4), mastoid width (v. 7.2), C^1-M^3 (v. 4.2), dentary length (v. 8.7), radius length (v. 33.5), tibia length (v. 13.7); however rostrum longer (5.1 v. 4.2) and narrower as indicated by RC^1-LC^1 and anteorbital width relative to rostrum length (v. 1.02 and v. 0.98, respectively); posterior palate wider (1.7 v. 1.4); distance between bullae wider (1.3 v. 0.7); frontals more concave; postpalatal spine much smaller; sphenorbital sinus not extending anterior to posteropalatal margin; posteronarial opening more oval in outline; mesial margin of cochlea smooth and not angular; baculum much shorter (v. > 11), shaft straight not sinuous.

Description (mean and range)

Skull and Dentary (Figure 12)

Small fragile skull: greatest skull length 11.9 (11.1-12.5), zygomatic width 7.9 (7.6-8.3), interorbital width 3.5 (3.3-3.7), mastoid width 7.0 (6.6-7.4), dentary length 8.4 (8.0-8.9). Similar to *P. westralis* in: dorsal profile of skull, rostral depression, anterior nares, supraorbital tubercles, anteropalatal emargination, infraorbital foramen, lachrymal bar, absence of sagittal crest, weakness of lambdoidal crest, zygoma, palatal depression, postpalatal spine, mastoid, pterygoid process, shape of glenoid surface for mandibular condyle, dental cusp and cingular morphology. Posterior palate moderately wide 1.7

(1.4-1.8), low; medium septum supporting posterior palate moderately wide, short, vertical, not visible behind posteropalatal margin when viewed vertically; outline of posteronarial openings oval to elongate, usually just visible behind posteropalatal margin when viewed vertically; sphenorbital sinus moderately flared laterally, terminates level with, or posterior to, posteropalatal margin; slight to moderate median presphenoidal groove. I^2 usually less than height of posterior cusp I^1, not extruded from line of tooth row; C^1 posterior cutting edge slight to moderate angle to line of tooth row and with small to moderate posterior basal cusp, base oval; P^2 surface area subequal to I^2, less than half height P^4; P_2 two-thirds height and four-fifths surface area P_4, slightly extruded from tooth row.

External Morphology

Small delicate, as for *P. adamsi* except that basal lobe of tragus frequently not as developed; snout to anus length 38.6 (33.9-41.8), tail length 28.3 (24.0-32.7), tibia length 12.0 (10.9-13.2), pes length 5.5 (4.9-6.5), ear length 10.5 (8.4-11.8), tragus length 5.2 (3.5-5.9).

Pelage and Skin

Described from dried alcohol preserved specimens. Dorsum Bone Brown of tips, basal two-thirds Fuscous Black. Ventral surface Cinnamon Brown of tips, basal three-quarters Fuscous Black. Snout, lips, ears, patagia, forearms, pes, Clove Brown. Uropatagium lightly furred with Cinnamon Brown along venation; plagiopatagium lightly furred under humerus.

Glans Penis

Penis length 4.9 (4.7-5.2); glans similar to *P. adamsi* but with distal projecting lobe shorter, broader, and dorsal distal folds frequently very reduced, preputial attachment approximately 1 mm from distal end of glans (Figure 5e).

Baculum

Short 1.97 (1.82-2.10) (N = 5 — adults only) with broad base 0.72 (0.67-0.76), shaft relatively broad, not curved, last 10-20% bifurcated (Figure 6e). Relationship between total length (L) and basal width (W) including 9 juveniles is $L = 1.53W + 0.88$ ($r = 0.93$, $N = 14$, $p < 0.1$) (Figure 9).

Distribution

Widely distributed in coastal and highland mainland Papua New Guinea and associated islands (e.g. Fergusson). Probably widespread also in Irian Jaya and associated islands (e.g. Kei = Kai I.) (Figure 7).

Specimens Examined

Papua New Guinea: Ambunti (4°13′S, 142°50′E), 2♂, CM1986, CM1988(J); Avatip (4°09′S, 142°58′E), 1♂, CM 4505(J); Fergusson I. (9°30′S, 150°30′E), 2♀, JM4962-3; Karimui (6°30′S, 144°45′E), 6 ♀, SAM M10565, SAM M10573-4, SAM M10579, SAM M10586-7; Korogo (4°06′S, 143°09′E), 2♂, CM4522(J), CM4919(J); Mt Lamington (8°56′S, 148°10′E), 1♀2♂, SAM M2838/001-002; SAM M2838/004; Mt Lamington 'Division' (*c.* 8°56′S, 148°10′E), 4♀3♂, AM 4179, AM 4181, AM4314-6, AM10081, AM10086; Rave-Kivau (7°15′S, 145°10′E), 1♀, CM1938; Safia (9°36′S, 148°39′E), 1♀, CM1824; Tepala (8°05′S, 146°12′E), 3♀4♂, CM1945, CM1947-8, CM1954-5(2J), CM1958(J), CM1959; 'Yagaum', 1♂, CM16028.

Irian Jaya: Salawatti (*c.* 1°00′S, 130°50′E), 1♀, MSNG 11660 (holotype).

Referred Specimens (not measured)

Papua New Guinea: 'D'Entrecasteaux I.', 1♀, BM 95.5.8.3; 'Webi', 1♀, BM 29.5.27.10; 'Chads Bay', 2 ?sex, BM99.12.3.5-6; 'S of Huon Gulf' 1?sex, BM 76.7.5.9. 'Gira', 1?sex, BM 6.1.8.30, 'Mambare R.' 1♀, BM 6.1.8.2.

Irian Jaya: Kei I (= Kai Is). (*c.* 5°30′S, 130°00′E), 1?sex, BM 10.3.1.72.

Pipistrellus wattsi sp. nov.

Figures 5f, 6f, 7, 9, 13, 18; Tables 1 and 3

Holotype

CM1946, adult female, body in alcohol and skull separate, from Tepala, Papua New Guinea (8°05′S, 146°12′E), collected by L. Craven, 1 March 1966.

Paratypes

Listed in Specimens Examined.

Diagnosis (mean values)

Differs from *P. westralis* in that its skull, dentary and teeth are larger for most characters: greatest skull length (11.6 v. 11.4), mastoid width (7.1 v. 6.7), C^1M^3length (4.1 v. 3.9), narrower posterior palate (1.3 v. 1.6); rostrum broader, as indicated by width of $RC^1 LC^1$ and anteorbital distance relative to rostrum length (0.82 v. 0.77, 0.82 v. 0.77, respectively); postpalatal spine longer, broader; posterior margin of palate higher such that posterior nares subcircular in outline rather than elongate; sphenorbital sinus terminates level with or posterior to the posteropalatal margin rather than extending anterior to this margin; radius longer (30.9 v. 28.9); ears more rounded at apex; tragus posterior edge more convex; glans penis with single distal fleshy tongue rather than distal fleshy spines; baculum shorter (2.67 v. 3.02), broader base (0.72 v. 0.68) (Figure 9), lateral profile of shaft straight rather than considerably curved, distal bifurcating prongs 10% rather than 30% of baculum length.

Differs from *P. adamsi* in that nearly all measurements recorded average smaller: greatest skull length (v. 12.0), C^1M^3 (v. 4.4), $RM^3 LM^3$ (5.1 v. 5.5), dentary length (8.3 v. 8.9); rostrum shorter relative to greatest skull length (0.42 v. 0.45), and broader as indicated by width of $RC^1LC^1$and anteorbital distance relative to rostrum length (v. 0.78, v. 0.74,

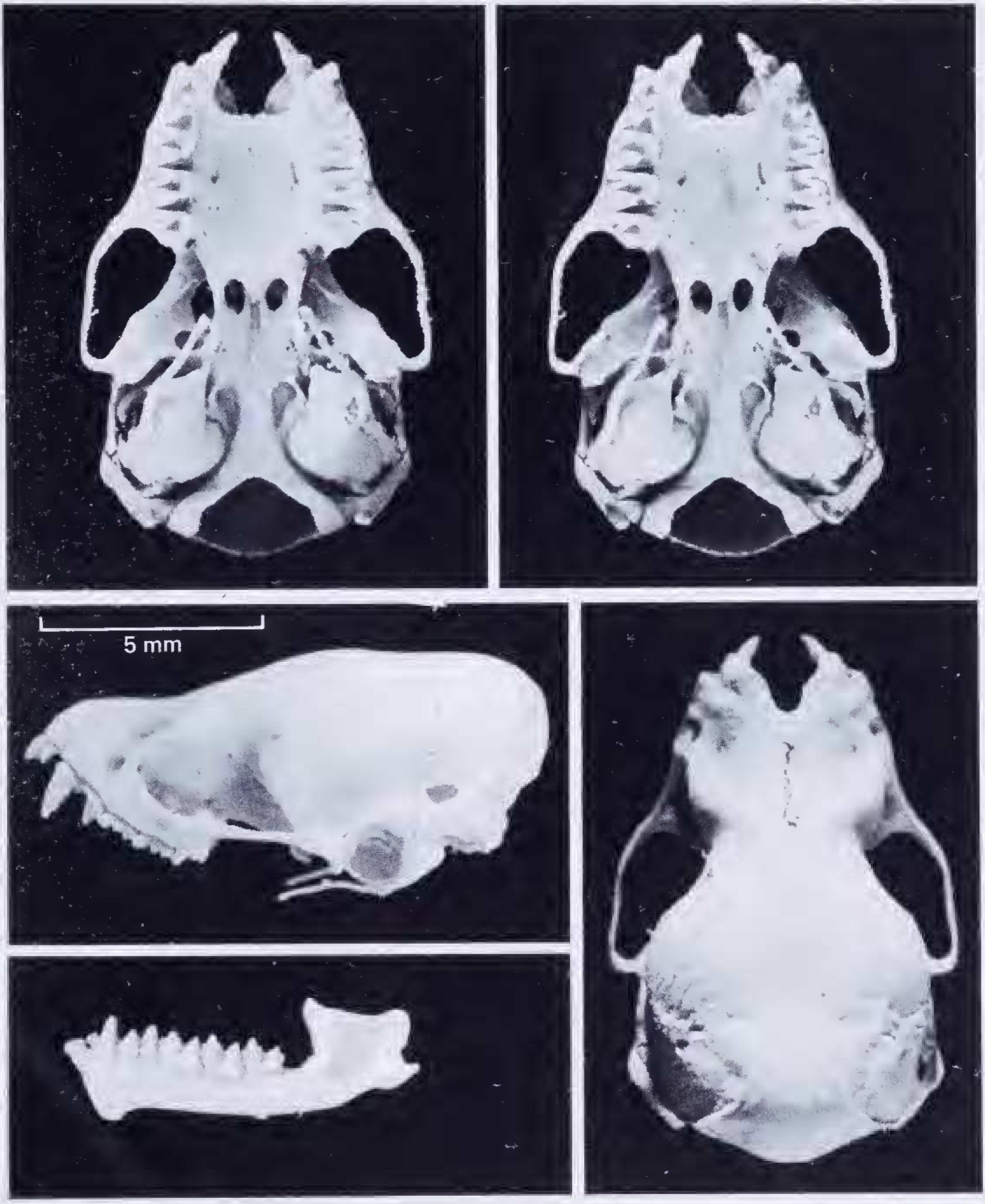

Figure 13 Skull and dentary of *Pipistrellus wattsi* (CM 1946, holotype). Ventral view of skull as stereopairs.

respectively); braincase broader relative to greatest skull length (0.56 v. 0.53); postpalatal spine much larger.

Differs from *P. papuanus* in that the posterior palate is narrower relative to palatal length (0.25 v. 0.33); rostrum broader as indicated by width RC^1LC^1 and anteorbital distance relative to rostrum length (v. 0.78, 0.73, respectively); postpalatal spine larger; anteropalatal emargination larger; baculum longer (v. 1.97), base narrower relative to its length (0.27 v. 0.37) (Figure 9).

Differs from *P. angulatus* in that the skull is shorter (v. 12.2), brain case, mastoid and interorbital regions wider relative to greatest skull length (v. 0.52, 0.61 v. 0.56 and 0.32 v. 0.28, respectively); rostrum broader and narrower as indicated by width of RC^1-LC^1 and anteorbital distances relative to rostrum length (v. 0.73 and v. 0.71, respectively); anteropalatal emargination larger; face of skull much less concave; radius shorter (v. 32.8); tail shorter (29.5 v. 32.1); tibia shorter (12.1 v. 13.5); distal end of glans penis broader with more prominent distal fleshy lobe; baculum much shorter (v. 3.48) but with bases of similar width (both 0.72), shaft narrower (Figure 9).

Differs from *P. collinus* in that most skull, dentary, teeth and external measurements are shorter: greatest skull length (v. 13.2), mastoid width (v. 7.5), C^1-M^3 (v. 4.7), RM^3-LM^3 (v. 5.8), dentary length (v. 9.4). The shape of the skull differs in that the following measurements are greater relative to greatest skull length: interorbital width (v. 0.26), braincase width (v. 0.52); rostrum broader as indicated by width of RC^1-LC^1 and anteorbital distance relative to rostrum length (v. 0.79, v. 0.77, respectively); baculum much shorter (v. 4.47), base narrower (v. 0.82) (Figure 9).

Differs from *P. tenuis, P. javanicus* and *P. imbricatus* in the same way that *P. adamsi* differs from these species.

Description (mean and range)

Skull and Dentary (Figure 13)

Small fragile skull: greatest skull length 11.6 (11.1-12.5), zygomatic width 7.9 (7.4-8.4), mastoid width 6.9 (6.4-7.4), dentary length 8.3 (7.8-9.0); similar to *P. adamsi* in shape of dorsal profile of skull, rostral depression, supraorbital tubercles, infraorbital foramen, lachrymal bar, absence of sagittal crest, weak lambdoidal crest, zygoma, palatal depression, mastoid, pterygoid process, shape of glenoid surface for mandibular condyle, dental cusp and cingular morphology. Interorbital width 3.7 (3.5-3.9), anterior nares arrow-shaped, deep, extending to posterior margin of infraorbital foramen; braincase wide 6.5 (6.1-6.8); anteropalatal emargination wide and deep, extending to centre of P^2; posterolateral palatal bones surrounding posteronarial passages only very slightly inflated; postpalatal width narrow 1.3 (1.2-1.4), relatively high above sphenoid; posterior median septum supporting palate relatively tall and moderately wide, almost vertical; outline of posterior nares subcircular, moderately large; median septum and opening of nares not visible behind posteropalatal margin when viewed vertically; slight median presphenoid groove; moderate to large rectangular foramen on either side of presphenoid extending from immediately posterior to opening of posterior nares to level with base of pterygoid process; postpalatal spine long, reaching approximately to middle of zygomatic arch; basisphenoid depressions shallow to moderately deep; sphenorbital sinus considerably flared laterally such that it is subcircular in outline, extends level with posterior margin of palate; I^1 bicuspid; I^2 usually just reaching posterior cusp I^1, not extruded from line of tooth row; C^1 posterior cutting edge at slight angle to tooth row with small to moderate basal cusplet; P^2 subequal or slightly larger than surface area of I^2; metacristid M^{1-2} subequal in length; P_2 three-quarters height and four-fifths surface area P_4, four times surface area I_3, barely extruded from line of tooth row.

External morphology

As for *P. adamsi*. Small, delicate: snout to anus length 37.3 (36.0-40.0), tail length 29.5 (27.6-31.6), tibia length 12.1 (11.7-12.9), pes length 5.4 (4.8-6.0), ear length 10.9 (10.0-12.0), tragus length 5.3 (4.8-5.7).

Pelage and Skin

Described from dried alcohol preserved specimens. Dorsum Bone Brown of tips, basal two-thirds Fuscous Black. Ventral surface Pinkish Buff of tips, basal two-thirds Fuscous Black. Chin and throat Pinkish Buff hairs. Snout, lips, ears, patagia, forearms, pes, Chaetura Drab. Ventral surface uropatagium lightly furred with Pinkish Buff along veins; plagiopatagium beneath humerus heavily furred with Pinkish Buff.

Glans Penis and Baculum

Glans penis (Figure 5f) similar to *P. adamsi*. Baculum length 2.67 (2.56-2.88) (N=4), width 0.72 (0.67-0.76) (Figure 6f).

Distribution

Southeast Papua New Guinea coast and Samari I. (Figure 7).

Etymology

Named after Christopher Henry Stuart Watts, Evolutionary Biology Unit, South Australian Museum.

Specimens Examined

Paratypes

'New Guinea', 1 ♂, C9718; Port Moresby (9°29′S, 147°09′E), 1 ♂, CM4093; Rave-Kivau (7°15′S, 145°10′E), 1 ♀, CM 1939; Tepala (8°05′S, 146°12′E), 2 ♂, CM1956-7; Rigo (9°48′S, 147°34′E), 1 ♂, AM3815.

Referred Specimens (not measured)

Dinner I. (= Samaria I.), S.E. New Guinea (9°40′S, 150°49′E), 1♀, BM 88.3.16.1; Kamali, mouth of Kemp Welch R. (10°03′S, 147°43′E), 2?sex, BM 97.8.7.22-23.

Pipistrellus angulatus (Peters, 1880)

Figures 5g, 6g, 7, 14, 18; Tables 1 and 3

Vesperugo angulatus Peters, 1880: Sitz. Ges. naturf. Freunde, p. 122.

Pipistrellus ponceleti Troughton, 1936: Rec. Aust. Mus. 19: 351, Bougainville I., Papua New Guinea.

Holotype

Adult female No. 5492 (Mus. Berol.) Duke of York I., between New Britain and New Ireland.

Diagnosis (mean values)

Differs from *P. westralis, P. adamsi, P. papuanus* and *P. wattsi* as detailed in earlier diagnoses.

Differs from *P. tenuis (sensu stricto)* in that it is larger in most measurements: greatest skull length (12.2 v. *c.* 10.9), C^1-M^3 (4.3 v. 3.7), dentary length (8.5 v. 7.3), radius length (32.8 v. 26.4), tibia length (13.5 v. 10.4); however, narrower posterior palate (1.4 v. 1.6), distance outside bullae (6.2 v. 6.4) and canine basal width (0.6 v. 0.7); P^2 larger; frontals more concave; posterior palate not as elevated above sphenoid, posteronarial openings very much smaller, outline elongate rather than subcircular; lateral and ventral bones surrounding posterior narial passages not inflated; posterior narial septum wider, shorter, vertical; septum and cranial inflection of narial passage not visible behind posteropalatal margin when viewed vertically; sphenorbital sinus projects slightly anterior, rather than level with or posterior to posteropalatal margin; postpalatal spine smaller.

Differs from *P. collinus* in that the skull, dentary and teeth are shorter in all characters: greatest skull length (v. 13.2), mastoid width (6.9 v. 7.5), C^1-M^3 (v. 4.7), RM^3-LM^3 (5.2 v. 5.8), dentary length (v. 9.4); radius length (v. 37.2); tibia shorter (v. 15.4); baculum much shorter (3.48 v. 4.47), base narrower (0.72 v. 0.82) (Figure 9) and not as markedly notched ventrally, shaft not as markedly curved in region of distal prongs.

Differs from *P. javanicus* in that it is smaller in most measurements: greatest skull length (v. 13.1), mastoid width (v. 7.5), C^1-M^3 (v. 4.9), dentary length (v. 9.5), radius length (v. 33.2); however, digit III, phalanges I and II lengths longer (12.3 v. 12.0 and 10.6 v. 10.0, respectively); lateral profile of face much more concave; skull proportions similar but rostrum narrowing more anteriorly as indicated by RC^1-LC^1 and anteorbital width relative to rostrum length (0.72 v. 0.80 and 0.71 v. 0.80, respectively), posterior palate narrower relative to palatal length (0.25 v. 0.30); outline of posterior nares not as elongate; lambdoidal crest much weaker in occipital region; glans penis with narrower and longer central distal fleshy lobe without small spicules; baculum much shorter (v. $>$ 5.0) with broader base and shaft relatively less curved.

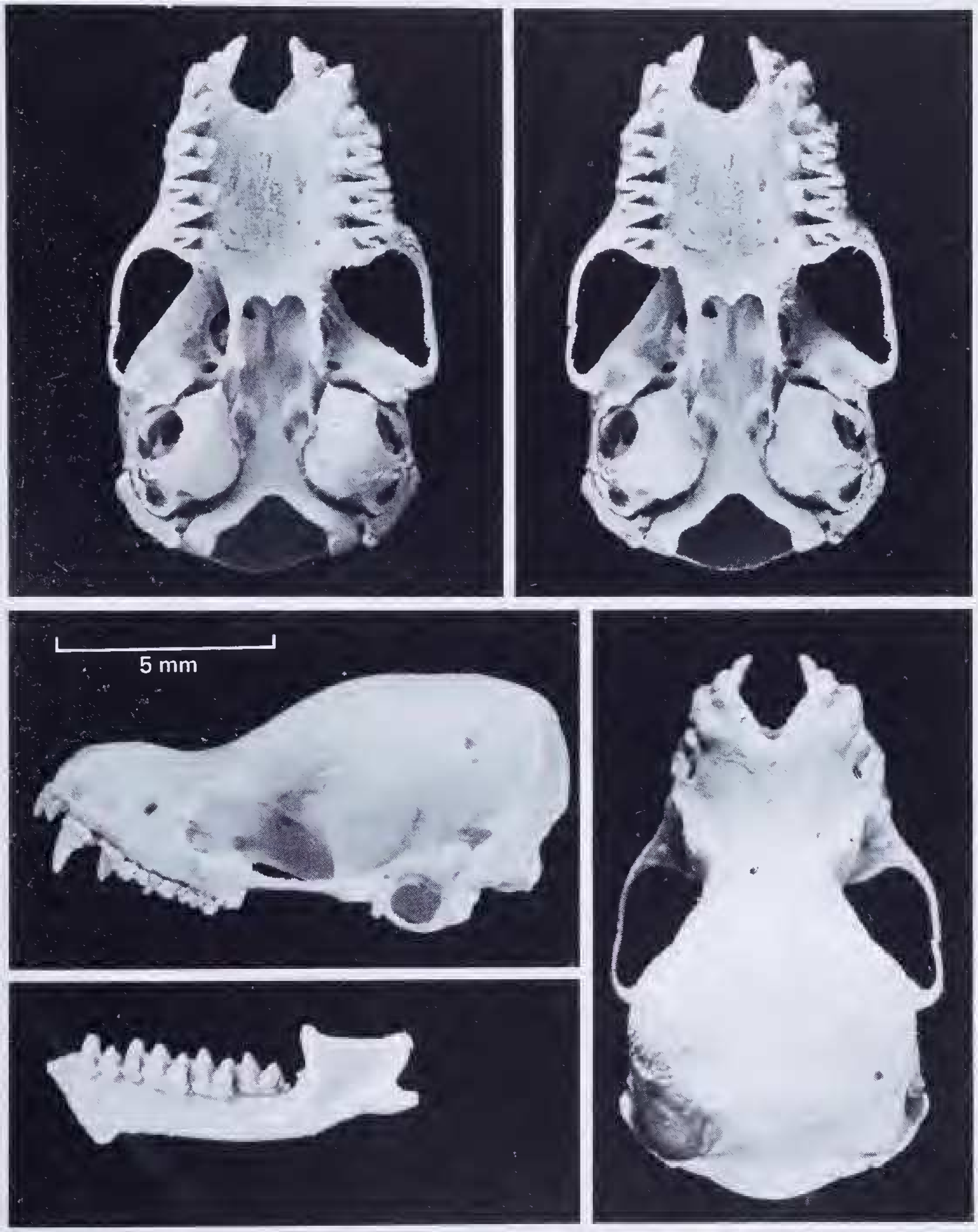

Figure 14 Skull and dentary of *Pipistrellus angulatus* (C 5429, topotype). Ventral view of skull as stereopairs.

Differs from *P. imbricatus* in that it is smaller in most measurements: greatest skull length (v. 12.4), mastoid width (v. 7.2), C^1-M^3 (v. 4.2), dentary length (v. 8.7), radius length (v. 33.5), tibia length (v. 13.7); however, distance between bullae larger (1.3 v. 0.7); rostrum narrower as indicated by RC^1-LC^1 and anteorbital width relative to rostrum length (v. 1.02, v. 0.98 respectively); frontals more concave and rise more sharply in interorbital region; P^2 much larger; anteropalatal emargination much smaller; posterior palate narrower relative to palatal length (v. 0.27); postpalatal spine smaller; outline of posterior narial opening more elongate; mesial margin of cochlea smooth and not angular.

Description (mean and range)

Skull and Dentary (Figure 14)

Moderate size: greatest skull length 12.2 (11.9-12.5), zygomatic width 7.6 (7.3-7.8), mastoid width 6.9 (6.6-7.7), dentary length 8.5 (8.1-8.8); dorsal profile of skull with very concave rostrum immediately posterior to premaxilla, rising sharply in interorbital region to approximate mid-point of parietal, then sloping gently downwards to interparietal; slight to moderate median rostral depression; anterior nares arrow-shaped terminating anterior to line joining infraorbital foramen; supraorbital tubercles slight to absent; interorbital width narrow 3.4 (3.2-3.7); rostrum long 5.1 (4.8-5.5) and narrow as indicated by anteorbital width 3.6 (3.4-3.7); infraorbital foramen small, subcircular; lachrymal bar wide; sagittal crest absent; lambdoidal crest moderate laterally, decreasing in height towards supraoccipital, absent from apex; zygoma moderately wide at base but weak in middle; braincase narrow 6.4 (6.1-6.7); anteropalatal emargination shallow, semicircular, or square, reaching to anterior edge P^2; palatal depression moderate; posterior palate moderately wide 1.4 (1.3-1.5), moderately high above sphenoid, extends posteriorly such that viewed vertically it covers base of median palatal septum and openings of posterior nares; posterior nares moderately large, oval in outline; median septum supporting posterior palate usually moderately wide, short, vertical; postpalatal spine small; pterygoid process moderately long, triangular, apex acute and sharply recurved posteriorly; sphenorbital sinus moderately flared laterally, extends level with or slightly anterior to posteropalatal margin; glenoid surface for condyle of mandible approximately square in outline; presphenoidal median depression moderate; basisphenoid depression small, elongate and moderately shallow; bulla moderately long 2.6 (2.5-2.8), cover two-thirds cochlea. I^1 bicuspid; I^2 height subequal to that of I^1 posterior cusp; C^1 posterior cutting edge at slight to moderate angle to line of tooth row, with basal cusp absent or miniscule and a moderately wide basal flange; C^1 basal area elongate; P^2 less than half height P^4, surface area subequal or less than that of I^2, slightly intruded from line of tooth row; M^{1-2} metacrista subequal in length. P_2 two-thirds height and three-quarters surface area of P_4, slightly extruded from line of tooth row; other aspects of dental and cingular morphology as for *P. westralis*.

External Morphology

Small, robust: snout to anus length 38.2 (34.7-41.4), tail length 32.1 (27.7-36.0), tibia length 13.5 (12.8-14.0), ear length 11.2 (9.8-12.1), tragus length 5.7 (5.2-6.3), pes length 5.9 (5.3-6.7); ear triangular, apex rounded, posterior edge markedly concave; tragus narrowing only slightly at apex which is rounded, anterior edge slightly concave, posterior edge gently convex, basal lobe small; supratragus small, projects laterally to meet tragus two-thirds up its length; antitragus moderately high, semicircular, thin; other externals as in *P. westralis*.

Pelage and Skin

As for *P. papuanus*.

Glans Penis

Penis length *c.* 5; narrow glans penis with slight ventral folds forming shallow mesial groove to a point level with preputial attachment (approximately 1 mm from distal end); moderately broad fleshy lobe from dorsal rim of urethral opening but barely projected above rim (Figure 5g).

Baculum

Long 3.48 (3.30-3.61), base narrow, 0.77 (0.65-0.95), shaft narrow, flat or very slightly sinuous, distal 10% bifurcated (Figure 6g). Relationship between maximum length (L) and basal width (W) is $L = .91W + 2.78$ ($r = .80$, $N = 6$, $p < .05$) (Figure 9).

Distribution

Papua New Guinea - coastal and upland regions, Duke of York I., Bougainville I. (Figure 7).

Specimens Examined

Papua New Guinea: Ambunti (4°13′S, 142°50′E), 1 ♀, CM1980; Dogwa (8°53′S, 143°04′E), 2 ♀, C946, C948; Duke of York I. (4°10′S, 152°23′E), 1 ♀, C5429; Keita (6°08′S, 155°38′E), 1 ♀ 3 ♂, C7482-4, CM2127; Lohiki (7°32′S, 145°28′E), 1 ♀, CM1937; 'Mt Lamington Division', 1 ♀, AM7983; Rave-Kivau (7°15′S, 145°10′E), 1 ♀ 1 ♂, CM1950-1; 'Pukago Sepik Plains', 3 ♀ 3 ♂, AM10083-4, AM10087-91; Bougainville I., 1 ♂, AM5799.

Pipistrellus collinus Thomas, 1920

Figures 6h, 9, 15; Table 1

Pipistrellus papuanus collinus Thomas, 1920: Ann. Mag. nat. Hist. (9) 6: 533.

Holotype

Adult male BM 13.11.7.4. skull and skin, from Bihagi, head of Mambare River, British Papua (= Papua New Guinea) (8°04′S, 148°01′E), collected by A.S. Meek, 13 April 1906.

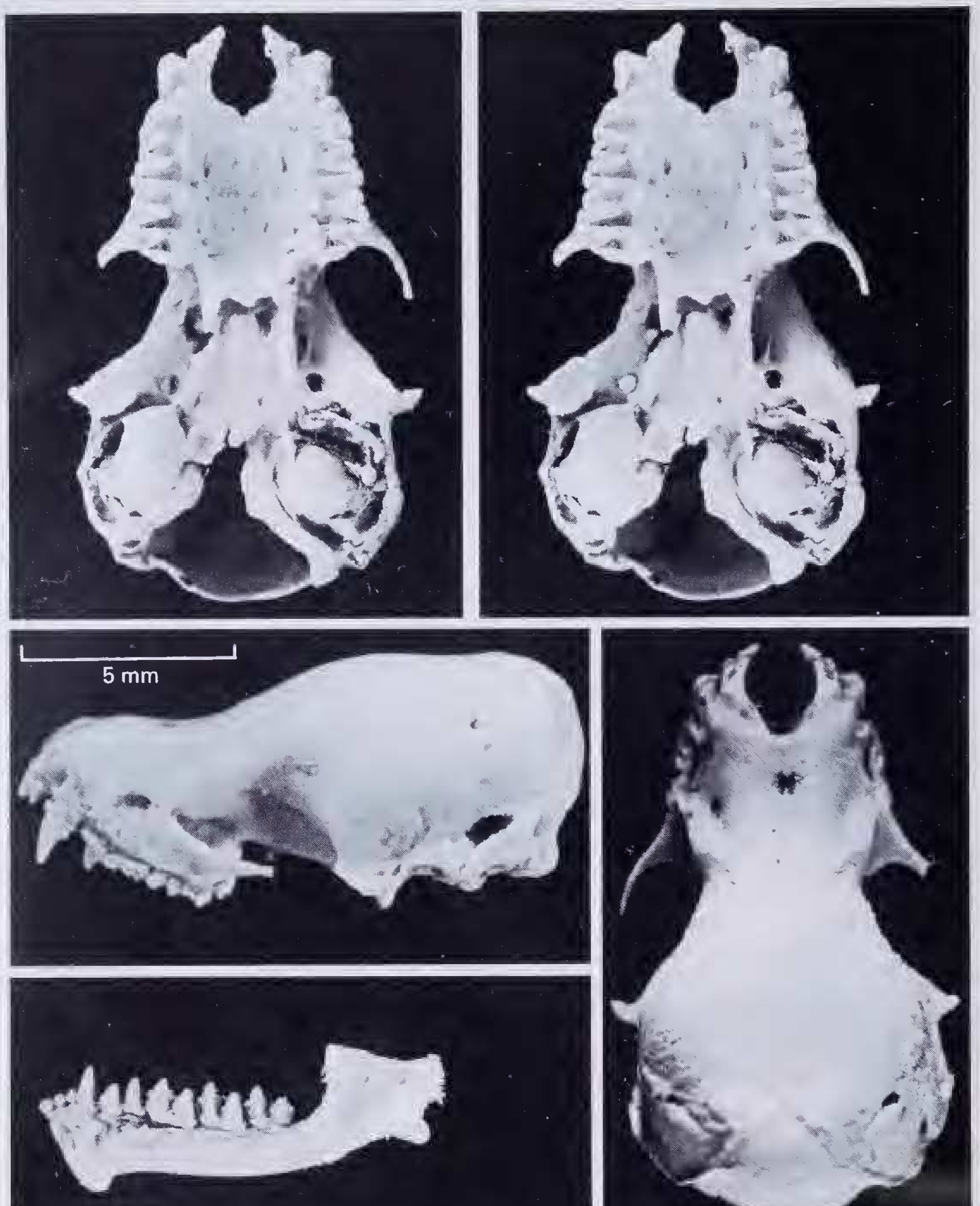

Figure 15 Skull and dentary of *Pipistrellus collinus* (CM 1638). Ventral view of skull as stereopairs.

Diagnosis (mean values)

Differs from *P. westralis, P. adamsi, P. papuanus, P. wattsi* and *P. angulatus* as detailed in earlier diagnoses.

Differs from *P. tenuis* as detailed for *P. angulatus* but with all measurements larger.

Generally similar in size to *P. javanicus* but with rostrum narrower as indicated by anteorbital width relative to rostrum length (0.77 v. 0.80); frontals more concave; lambdoidal crest much weaker in occipital region; postpalatal width narrower relative to palatal length (0.27 v. 0.30); outline of posterior nares oval rather than elongate; radius longer (37.2 v. 33.2); tibia longer (15.4 v. 13.3); baculum shorter (4.47 v. $>$ 5) with relatively narrower base which is notched in profile rather than smoothly curved.

Differs from *P. imbricatus* in being generally larger: greatest skull length (13.2 v. 12.4), mastoid width (7.5 v. 7.2), C^1-M^3 (4.7 v. 4.2), lower tooth row (6.0 v. 5.4), radius length (v. 33.5), tibia length (v. 13.7); shape of skull considerably different with longer palate relative to greatest skull length (0.45 v. 0.42); rostrum narrower as indicated by RC^1-LC^1 and anteorbital width relative to rostrum length (0.79 v. 1.02, 0.77 v. 0.98 respectively); rostral depression of frontals more marked, rise in lateral profile of rostrum sharper in interorbital region; anteropalatal emargination smaller; outline of opening of posterior nares much larger and posterior palate more elevated above sphenoid; P^2 much larger; distance between bullae much larger (1.3 v. 0.7); mesial margin of cochlea smooth and not angular; baculum much shorter (4.5 v. $>$ 11), shaft moderately curved, not sinuous.

Description (mean and range)

Skull and Dentary (Figure 15)

Large: greatest skull length 13.2 (12.9-13.5), zygomatic width (8.8), mastoid width 7.5 (7.4-7.6), dentary length 9.4 (9.1-9.7); general shape of skull, dentary and teeth very similar to *P. angulatus;* anterior nares narrow arrow-shape terminating level to anterior edge of infraorbital foramen; supraorbital tubercles absent; interorbital width moderate 3.5 (3.3-3.8); sagittal crest absent; lambdoidal crest moderate laterally but absent at apex; mastoid moderate; anteropalatal emargination semicircular reaching to mid point of P^2; palatal depression shallow; postpalatal width narrow 1.6 (1.5-1.8), moderately high above sphenoid, extends posteriorly such that viewed vertically it covers base of median palatal septum and openings of posterior nares; posterior nares moderately large, oval in outline; median septum supporting posterior palate usually moderately wide, short, vertical; dorsolateral bones of posterior palate surrounding narial passages only slightly inflated; postpalatal spine small; pterygoid process moderate, apex slightly recurved posteriorly; sphenorbital sinus very slightly flared laterally, extends level to posteropalatal margin; glenoid surface for mandibular condyle longer than wide; bulla relatively short 3.1 (3.0-3.1); short, acute eustachian projection, covers two-thirds of cochlea; basisphenoid depressions small, shallow; I^1 moderately high, I^2 taller than I^1 posterior cusp, not extruded from line of tooth row; C^1 posterior cutting edge with small basal cusplet in line with tooth row, base irregularly oval-shaped; P^2 one-third height P^4, surface area subequal to I^2; paracrista length increases M^{1-3}; metacrista M^{1-2} subequal lengths.

P_2 three-quarters height and three-quarters surface area of P_4, very slightly extruded from line of tooth row. Other aspects of dental and cingular morphology as for *P. westralis.*

External Morphology (only dried 'puppet' skins available for study)

Moderate size, slender: radius length 37.2 (35.7-39.1); tibia length 15.4 (14.2-16.4); pes length 7.6 (6.5-8.4); ears with very convex leading edge, apex broadly rounded; tragus with slightly concave anterior edge and gently convex posterior edge, apex rounded (basal lobe not visible); supratragus lateral projection at about level of two-thirds length of tragus (antitragus not visible). Calcar and its lobe, plagiopatagial attachment to digit of pes as for *P. westralis.*

Pelage and Skin

Described from 'puppet' skin. Dorsum Bone Brown from tips, basal two-thirds Fuscous Black, interspersed with frequent white hairs. Ventral surface Buffy Brown of tips, basal three-quarters Fuscous Black. Snout, lips, ears, patagia, forearms, pes, Clove Brown. Uropatagium lightly furred with Buffy Brown along venation.

Glans Penis

Not seen.

Baculum

Long 4.47, base narrow 0.82 (Figure 9), with pronounced ventral notch; shaft narrow, flattened dorsally, straight but for the last one-fifth which is moderately inflected dorsally, last 10% bifurcated.

Distribution

Central highlands, Papua New Guinea (Figure 7).

Specimens Examined

Papua New Guinea: Bihagi (8°04′S, 148°01′E), 1♂, BM 13.11.7.4 (holotype); Minj R., Kubor Ra., Central Highlands (6000 ft) (5°52′S, 144°38′E), 1 ♂, BM53.206; Upper Aroa R. (9°05′S, 146°48′E), 1?sex, BM 13.11.7.3; Baiyanka, Purari-Ramu Divide, S.E. Bismark Ra. (*c.* 7°46′S, 145°10′E), 1 ♂, BM 50.983; Aseki (7°20′S, 146°30′E), 1 ♀, CM1638.

Morphometric Analyses: Results and Discussion

Univariate Analyses

The means and standard deviations of the 37 skull and external characters by sex for the ten species are shown in Table 1.

The two factor ANOVA revealed significant sexual dimorphism in only 12 of the 37 characters examined ($p < .05$), with females the larger in each of these 12 characters. The 12 characters consisted of 11 skull variables (AOB, ZW, PL, BL, OB, RC^1-LC^1, M^2W, M^3W, RM^3-LM^3, LR, DL) and one external variable (HV).

Three of the 37 characters resulted in a significant interaction between sex and species. These were PL, IB and OB ($p < .05$).

Phenetic Analyses

Canonical Variate Analyses

Canonical variate analyses were used to examine the variation between the two species of *Falsistrellus* and the eight species of *Pipistrellus* for each of the sexes separately and combined using all the skull measurements (Figures 16a, b, c). The external measurements were not used at this stage because all specimens of *P. collinus* and *P. imbricatus* had an incomplete set of external body measurements.

In these analyses, *F. tasmaniensis* and *F. mackenziei* were clearly separated from the remaining species on the first canonical variate. *Pipistrellus collinus, P. imbricatus* and *P. javanicus* were clearly separated from other species on the first or second canonical variate. Also, the variation between sexes within species was generally much smaller than the variation between species, so that sexes were combined in subsequent analyses.

Because of clear differences between the *Falsistrellus* spp. and the eight *Pipistrellus* spp., further canonical variate analyses concentrated on discriminating between *F. tasmaniensis* and *F. mackenziei*, and also between the five species of *Pipistrellus* that cluster close together in Figure 16 (*P. westralis, P. adamsi, P. papuanus, P. wattsi* and *P. angulatus*).

A stepwise canonical variate analysis using all skull and external variables showed that *F. tasmaniensis* and *F. mackenziei* could be clearly identified (Figure 17, Table 2) on the following six characters: cranial height (CH), basicranial length (BL), bulla length (BUL), canine width (CW), dentary length (DL) and digit III, phalanx II length (PII).

Similarly, the five *Pipistrellus* species show a high degree of separation (Figure 18). When this analysis was repeated a number of times, leaving a randomly chosen ten percent of the specimens out of the sample each time, it resulted in an unbiased 'correct' classification of 95 percent. This analysis produces the following three canonical variate functions (Table 3): Variate I (explaining 42.6 percent of variance), which appears to be related to greatest skull length as well as postpalatal width and tooth row lengths, separates *P. westralis* and *P. papuanus* from *P. adamsi, P. wattsi* and *P. angulatus;* Variate II (30.6 percent) with greatest skull length and braincase width providing the maximum separation between *P. papuanus* and *P. westralis* and between *P. adamsi, P. wattsi* and *P. angulatus;* Variate III (18.7 percent) relates mostly to greatest skull length, palatal length, ear width and digit III, phalanx I length; it provides little further separation of the species. Although *P. wattsi* is clearly separate from these other species the sample was small (N = 7) and included only two females; more specimens of this species, particularly of females, would be desirable before supporting the diagnostic value of the separations.

Other Phenetic Analyses

There is general agreement in the clustering of the two *Falsistrellus* species and the eight *Pipistrellus* spp. produced from the minimum spanning tree and UPGMA cluster

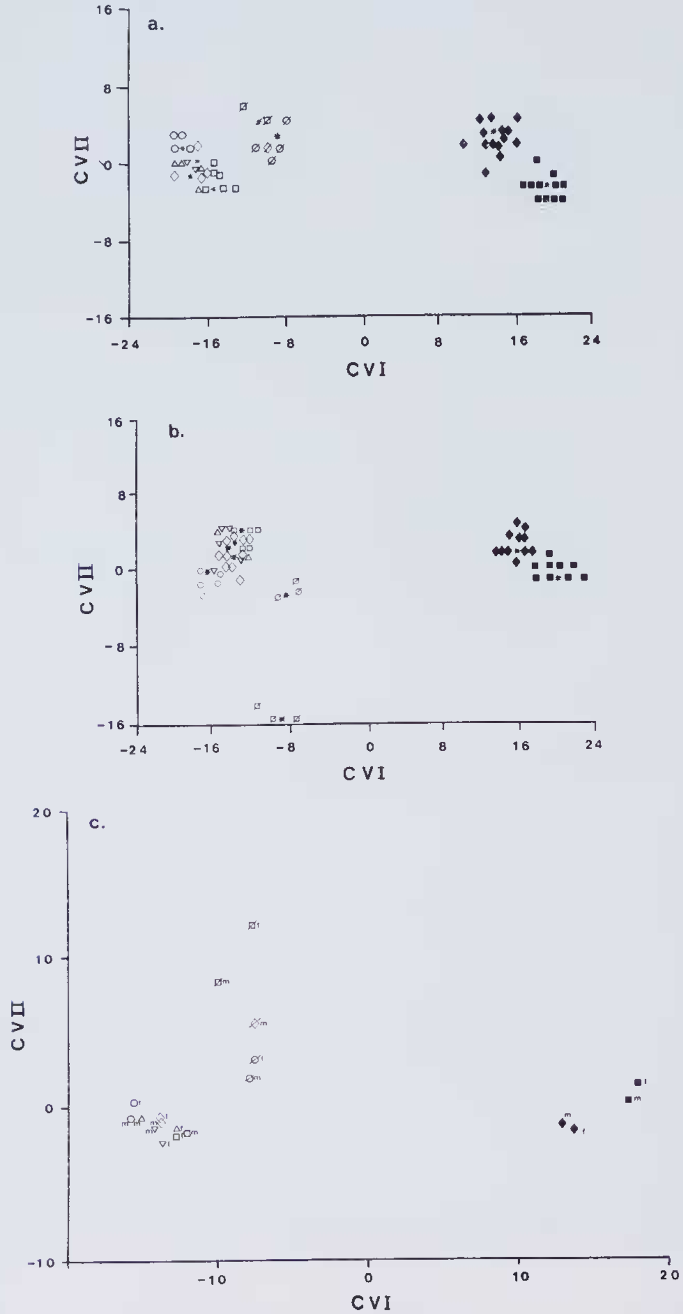

Figure 16 Canonical variate analyses based on skull measurements for *Falsistrellus tasmaniensis* (♦), *F. mackenziei* (■), *Pipistrellus westralis* (○), *P. adamsi* (□), *P. papuanus* (◇), *P. wattsi* (△), *P. angulatus* (▽), *P. collinus* (∅), *P. javanicus* (∅) and *P. imbricatus* (∅), showing the group means (*) for the first two variates for analysis of (a) males, (b) females, (c) males [m] and females [f]. The distribution of specimens about the group means are indicated for (a) and (b).

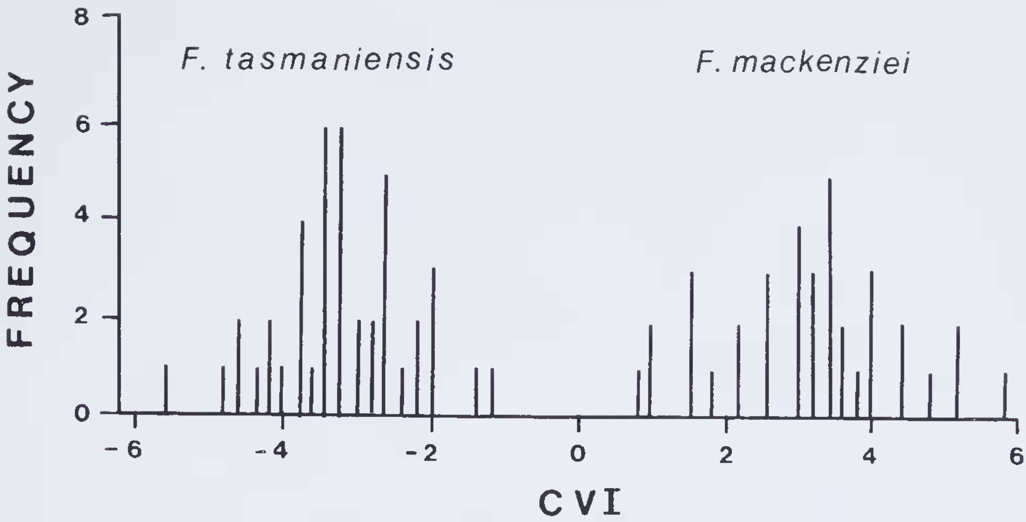

Figure 17 Stepwise canonical variate analyses based on skull and external measurements with sexes combined, for *Falsistrellus tasmaniensis* and *F. mackenziei* showing the distribution of specimens along the canonical variate. Six characters (sce Table 2) provide complete separation of these species.

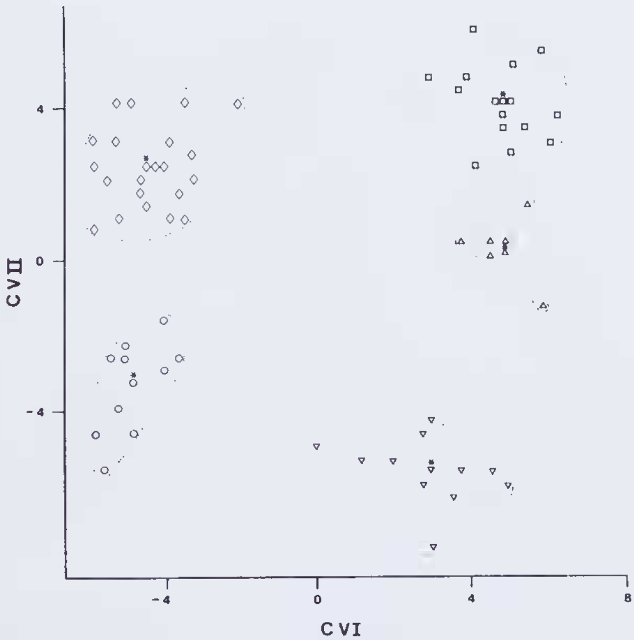

Figure 18 Canonical variate analysis based on all skull and external measurements for the five smaller pipistrelles: *P. westralis* (○), *P. adamsi* (□), *P. papuanus* (◇), *P. wattsi* (△) and *P. angulatus* (▽), showing the first two variates. The distribution of the specimens about the group means (*) are shown.

Figure 19 Phenetic relationships derived by UPGMA cluster analysis on *Falsistrellus* spp. and *Pipistrellus* spp. Males and females are combined and skull and dentary characters only are used. Species are symbolised as follows: *Falsistrellus tasmaniensis* (♦), *F. mackenziei* (■), *Pipistrellus westralis* (○), *P. adamsi* (□), *P. papuanus* (◇), *P. wattsi* (△), *P. angulatus* (▽), *P. collinus* (⌀), *P. javanicus* (⌀) and *P. imbricatus* (⌀).

analyses, whether using skull characters alone or skull plus external characters and whether the data was untransformed or size free. The phenogram shown (Figure 19) was produced from untransformed skull characters, which allows *P. collinus* and *P. imbricatus* to be included because we had complete measurements of only the skulls of these species. This phenogram shows that the *Falsistrellus* spp. cluster quite separately from the *Pipistrellus* spp. Within the pipistrelles the smaller species form a tight group (*P. westralis, P. wattsi, P. adamsi, P. papuanus* and *P. angulatus*), with the Australian species not clustering with each other but *P. westralis* with *P. papuanus* and *P. adamsi* with *P. wattsi*. *P. collinus* is closest to *P. javanicus* and then to *P. imbricatus*.

Figure 20 Wagner tree showing phylogenetic relationships of *Falsistrellus* spp. and *Pipistrellus* spp. Males and females are combined and skull and dentary characters only are used. Data are range coded. The tree is rooted using *Scotorepens greyii* as the outgroup.

Phylogenetic Analyses

The selection of an outgroup in phylogenetic analysis is of considerable importance and a matter of continuing debate (Griffiths 1983, Smith and Hood 1984 and numerous recent papers in *Systematic Zoology*). Maddison *et al.* (1984) stress that while distant outgroups can provide a decision for phylogenetic construction based on parsimony, the ancestral state assessment is more robust the closer and more comprehensive the outgroups are to the ingroup. Tate's (1942) phylogeny of the Vespertilioninae provides something of a framework for the selection of an outgroup in this study. Unfortunately Tate's phylogeny is based, at least in part, on symplesiomorphies and as such is suspect. We include the Nycticeiini *Scotorepens greyii* (Gray, 1843) and the Pipistrellini (*sensu* Tate) *Chalinolobus gouldii* Gray, 1841, as optional outgroups in this study. The Wagner tree (Figure 20) uses the former species as the outgroup and is based on untransformed skull characters alone (this allows *P. collinus* and *P. imbricatus* to be included). The topology of the tree is very similar, however, if skull plus external characters, and untransformed or size free data are used, or if *C. gouldii* is used as the outgroup (although with this latter species included in the analysis the tree is rooted closer to the *Falsistrellus* group).

The species included in *Falsistrellus* and *Pipistrellus* in this study form two monophyletic groups. These monophyletic groups are also separated by considerable patristic distances. The two Australian pipistrelles are not closest relatives *(P. westralis* is the sister species to *P. wattsi).*

P. collinus has been associated with *P. angulatus, P. papuanus* and *P. westralis,* by its frequent placement with them as subspecies of *P. tenuis.* It appears, however, to have speciated much earlier from the ancestor of this group and of the several other diverse species considered.

This phylogenetic analysis, and a previous one of Australian Nycticeiini (Kitchener and Caputi 1985), are principally aimed at showing the extent of the separation of *Falsistrellus, Scoteanax* and *Scotorepens* from associated genera, with the purpose of evaluating the case for the recognition of these genera. Both these analyses were based on linear measurements and as such some characters used to diagnose the genera studied were not reflected in the analyses. More detailed phylogenetic analyses utilising also discontinuous characters (both coded shape and meristic characters) may influence the phylogenetic separation between *Falsistrellus* and *Pipistrellus* and the genera studied in Kitchener and Caputi (1985).

The phylogenetic considerations reached in this study must be considered tentative pending a more detailed analysis which includes examination of a wider range of genera and of different sets of characters.

General Discussion

Electrophoretic data are available for four of the 11 species considered *(F. tasmaniensis, F. mackenziei, P. westralis* and *P. adamsi).* These data, which support the taxonomy proposed herein (M. Adams pers. comm), will be published separately by our colleagues at the Evolutionary Biology Unit, South Australian Museum.

The genus *Falsistrellus,* comprising the two species *F. tasmaniensis* and *F. mackenziei,* is phenetically and phylogenetically quite distinct from northern Australian and Irian Jaya/Papua New Guinea *Pipistrellus.*

Australian *Pipistrellus* are, however, phenetically and phylogenetically very close to South East Asian pipistrelles. Koopman (1973) in his appraisal of the systematics of Indo-Australian pipistrelles expanded the concept of *Pipistrellus tenuis* to include all the known New Guinea forms as well as *P. sewelanus, P. nitidus, P. subulidens* and *P. murrayi.* Koopman (1984) later included both northern Australian forms *(P. westralis* and *P. papuanus)* within *P. tenuis.* In New Guinea, Koopman (1973) extended the recognition by Laurie and Hill (1954) of a lowland form of *Pipistrellus (P. papuanus)* and a highland form *(P. angulatus collinus)* by considering these forms as part of an altitudinal cline. On the south coast where highland and lowland localities are well separated, lowland *P. papuanus* and highland *P. collinus* are readily distinguishable by skull size and to some extent by rostral dimensions. Koopman (1973) considered that these distinctions become less clear around the eastern end of the island and onto the north coast — such that in northeastern Irian Jaya *P. papuanus* and *P. collinus* form a single intergrading series. McKean and Price (1978), examined the bacula of New Guinea pipistrelles and also concluded that these named forms were subspecies of *P. tenuis.*

We do not agree with the above interpretation that the Australian and New Guinea pipistrelles are subspecies of *P. tenuis.* Our first concern is the placement of both Australian forms *(P. westralis* and *P. 'papuanus')* as subspecies of *tenuis.* We show that these forms are specifically distinct with overlapping ranges. Clearly, they both cannot be subspecies of *P. tenuis.* Close comparison of these Australian forms with the cotypes of *P. tenuis* from Sumatra, Indonesia, indicates them to be valid species. The eastern form is distinct from *P. papuanus* and is described herein as a new species *(P. adamsi).* The western form, which is quite distinct from *P. murrayi, P. sewelanus* or *P. nitidus,* is elevated to species rank. The evidence presented by Koopman (1973, 1982) that *P. collinus, P. angulatus* and *P. papuanus* form part of an altitudinal cline is far from convincing. His evidence was based on only three cranial measurements (condylobasal length, width across M^3, maxillary tooth row length) and shows the higher altitude specimens to be distinct in Papua (Koopman 1973: Figure 2) but not in Irian Jaya (his Figure 3). Regressions similar to those by Koopman referred to above are not uncommon in valid species in sympatry, where they result from usual allometric processes. The bacular data of McKean and Price (1978) are also unconvincing. They considered that a series of bacula from the forms *P. papuanus, P. ponceleti* and *P. collinus,* although varying greatly, were merely stages in ossification and growth. If this were true, then some measurements they showed would actually have to become reduced as the animal aged (*cf.* their Figures 1b and 1c). While such a reduction in measurements with ageing has been suggested for some cranial measurements (Kitchener and Foley 1985), it is highly unusual. We have examined the allometric relationship between baculum basal width and greatest length for the Papua New Guinea forms considered by McKean and Price (1978), including remeasuring most of the bacula they considered in their study (which appear asterisked in our Figure 9); the linear relationships between these two bacular measurements are indicated for *P. papuanus* and *P. angulatus.* Clearly the forms of bacula described by McKean and Price (1978: Figure 1a & b) are from a distinct species *(P. papuanus)* to that in their Figure 1c *(P. ponceleti)* and Figure 1d *(P. collinus).*

Our study shows that the few measurements used by Koopman (1973, 1982) are not diagnostic on their own for the taxa in question, but rather one must examine a much larger suite of characters, particularly emphasizing the shape of the posterior palate, glans penis and baculum. We conclude that *P. papuanus, P. angulatus* and *P. collinus* are valid species in Papua New Guinea and additionally name *P. wattsi* for that region.

We consider *P. collinus* a species, although we have seen few specimens, a single baculum and no glans penis. *Pipistrellus papuanus* is the species in the Australo-Papuan region most like *P. tenuis,* but it is considered too distinct for subspecific status within *P. tenuis.*

Koopman (1970) presents data which shows that while the Indo-Malay zoogeographic region has some 53 percent of the known species of *Pipistrellus*, the Australian region has only about 7%. It is, then, possible that the Australian pipistrelles evolved relatively recently from tropical forms. This recent evolutionary probability is supported by the observation that in Australia, pipistrelles retain a tropical distribution and that the two Australian species (*P. westralis* and *P. adamsi*) are not closest relatives; each is closer phenetically to Papua New Guinea species than they are to each other. These latter observations suggest that the Australian pipistrelles speciated independently from 'Papuan' ancestors, sometime during the late Cretaceous to early Pleistocene period during which the present island of New Guinea usually formed the northern edge of the original Australian continent (Ziegler 1977).

Although *Falsistrellus* appears to have evolved further than *Pipistrellus* from their common ancestor, this endemic Australian genus has speciated less. This reduced speciation in *Falsistrellus* may reflect its southern Australian distribution where it is restricted to closed forests and woodlands — a habitat that has shown an overall decline in extent in Australia since the late Tertiary (Galloway and Kemp 1984).

Key to *Falsistrellus* and Australo-Papuan *Pipistrellus* (measurements of adult males and females).

1 Greatest skull length more than 17 mm, marked occipital crest, I^1 unicuspid, I^2 considerably extruded from line of tooth row, C^1 broad at base, P_2 less than half height of P_4, radius length more than 45 mm, glans penis without terminal fleshy lobes or spines, baculum shaft almost as broad as its base .... *Falsistrellus* 2

Greatest skull length less than 14 mm, occipital crest weak or absent, I^1 bicuspid, I^2 little extruded from line of the tooth row, C^1 elongate at base, P_2 more than half height of P_4, radius length less than 40 mm, glans penis with terminal fleshy lobes or spines (*P. collinus* not observed), baculum shaft considerably narrower than its base .... *Pipistrellus* 3

2 Greatest skull length averages 18.3 (17.5-19.0), dentary length relative to basicranial length averages 0.86 (0.85-0.89), baculum basal width relative to its ventral length averages 0.40 (0.38-0.42) .... *Falsistrellus tasmaniensis*

Greatest skull length averages 19.2 (18.2-20.1), dentary length relative to basicranial length averages 0.90 (0.87-0.92), baculum basal width relative to its ventral length averages 0.47 (0.44-0.49) .... *Falsistrellus mackenziei*

3 Greatest skull length more than 12.5 mm, radius length more than 35 mm, baculum length more than 4 mm .... *Pipistrellus collinus*

Greatest skull length less than 12.5 mm, radius length less than 35 mm, baculum length less than 4 mm 4

4 Postpalatal width relative to palatal length more than 0.29 5

Postpalatal width relative to palatal length less than 0.29 6

5 Sphenorbital sinus extends anteriorly level with or posterior to edge of posteropalatal margin, glans penis with a single fleshy terminal lobe, baculum length less than 2.4 mm, baculum shaft straight in lateral profile, ratio of that part of the baculum that is bifurcated to the total length of baculum less than 0.20, tail length relative to snout to anus length less that 0.8 .... *Pipistrellus papuanus*

Sphenorbital sinus extends anterior to edge of posteropalatal margin, glans penis with more than one fleshy terminal spine or lobe, baculum length more than 2.4 mm, baculum shaft curved in lateral profile, ratio of that part of baculum that is bifurcated to the total length of baculum more than 0.25, tail length relative to snout to anus length more than 0.8 .... *Pipistrellus westralis*

6 Postpalatal spine long and extending posteriorly to approximately a line joining the mid-point of zygomatic arch .... *Pipistrellus wattsi*

Postpalatal spine short and extending posteriorly well short of a line joining the mid-point of zygomatic arch 7

7 Outline of posterior nares oval, rostrum rising sharply in interorbital region, radius length averaging 32.8 (31.1-34.8), baculum length greater than 3.0 mm, distribution Irian Jaya and Papua New Guinea .... *Pipistrellus angulatus*

Outline of posterior nares circular or subcircular, rostrum rising evenly in interorbital region, radius length averaging 31.0 (29.8-32.2), baculum length less than 3.0 mm, distribution Queensland .... *Pipistrellus adamsi*

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J. Paniperis typed the MS.

Appendix Measurements (in mm) of relevant type and unique specimens examined. See Figure 1 for description of characters. Preservation code: SS-skull and dry skin, SA-dry skull and body in alcohol.

Species, Catalogue No., type, sex, preservation / Character	*Vespertilio tenuis* BM 7.1.1.407, 'cotype', ?sex, SS.	*Vespertilio tenuis* BM 7.1.1.408, 'cotype', ♂, SS.	*Pipistrellus angulatus* C5429, 'topotype', ♀, SA.	*Pipistrellus ponceleti* AM M5799, paratype, ♂, SA.	*Pipistrellus collinus* BM 13.11.7.4, holotype, ♂, SS.	*Vespertilio tasmaniensis* BM 43.2.22.6, holotype, ?sex, SS.	*Vesperugo papuanus* MSNG 11660, holotype, ♀, SA.	*Pipistrellus murrayi* BM 99.8.6.34, holotype, ♂, SA.	*Scotophilus nitidus* BM 7.1.1.403, holotype, ?sex, SS.	*Vespertilio imbricatus* BM 79.11.21.108, holotype, ?sex, SA.	*Pipistrellus adamsi* JM 5022, holotype, ♂, SA.	*Pipistrellus wattsi* CM 1946, holotype, ♀, SA.	*Falsistrellus mackenziei* WAM 5149, holotype, ♂, SA.	*Pipistrellus javanicus* BM 47.7.21.12, 'Australia', ♀, SA.	*Pipistrellus javanicus* BM 47.7.21.13, 'Australia', ♂, SA.	*Pipistrellus westralis* WAM M22474, holotype, ♂, SA.
GL		10.9?	12.1	12.4	12.9		11.8	12.0			11.7	12.0	19.0	12.5	12.9	11.5
AOB	3.6	3.6	3.6	3.6	4.3	5.7	3.6	3.8	3.8	4.0	4.0	4.2	6.6	4.4	4.4	3.5
LOW		3.0	3.2	3.5	3.7		3.3	3.2	3.2	3.5?	3.6	3.6	5.0	3.7	3.6	3.5
ZW			7.6	7.6				7.6			8.1	8.0	13.4			7.5
ROL		4.5	5.1	5.2	5.3	7.3?	5.0	4.8	4.6	4.1	5.4	5.1	7.8	5.1	5.5	4.8
MW		6.8	7.0	7.6			6.9	7.2			7.0	7.1	10.5	7.7	7.5	6.9
BW		6.3	6.5	6.4	6.7		6.2	6.2			6.2	6.4	9.2	6.8	7.0	6.3
CH			4.6	4.5			4.4	4.7			4.5	4.5	7.4	4.8	4.8	4.5
PL		4.7	5.7	5.5	5.9		5.1	5.4	5.3		5.6	5.4	9.2	5.6	6.0	4.9
PPW		1.6	1.5	1.5	1.8		1.8	1.5	1.5		1.4	1.4	2.2	1.8	1.8	1.7
BL			10.2	10.2			9.8	10.0			10.0	9.8	16.3	10.2	11.0	9.5
BUL			2.5	2.6			2.6	2.8		2.9	2.7	2.7	3.7	3.0	3.0	2.7
BB			1.2	1.0			1.5	1.0			1.1	1.5	2.1	1.3	1.4	0.9
OB		6.4	6.2	6.1			6.4	6.3		7.1?	6.4	6.4	9.7	6.9	7.0	6.4
CW		0.7	0.7	0.5	0.8	1.0	0.6	0.8	0.8	0.9	0.6	0.5	1.3	0.8	0.9	0.5
RC^1-LC^1		3.5	3.9	3.8	4.4	5.6	3.9	3.7	3.6	4.0	4.1	4.1	6.8	4.3	4.5	3.4
C^1-M^3	3.7	3.7	4.6	4.4	4.7	6.7	4.2	4.3	4.1	4.1	4.3	4.1	7.4	4.6	4.9	3.8
M^1-M^3	2.6	2.5	3.0	2.8	3.2	4.5	2.7	2.7	2.7	3.0	2.9	2.6	4.9	3.0	3.2	2.5
M^2 L	1.0	1.0	1.1	1.1	1.3	1.7	1.1	1.1	1.0	1.1	1.1	1.0	1.9	1.2	1.3	1.1
M^2 W	1.2	1.2	1.3	1.1	1.4	1.9	1.2	1.3	1.3	1.5	1.3	1.2	2.1	1.5	1.4	1.2
M^3 W	1.3	1.0	1.4	1.2	1.6	2.0	1.2	1.4	1.3	1.3	1.2	1.1	2.0	1.4	1.5	1.2
RM^3-LM^3		4.7?	5.4	5.3	6.0	7.6	5.4	5.2		5.3	5.4	5.2	8.3	5.9	5.8	4.8
LR	4.7	4.6	5.7	5.5	6.0	8.1	5.1	5.4	5.4	5.0?	5.4	5.3	8.9	5.8	6.0	4.9
RC	2.0		2.4	2.4	2.9		2.5	2.4	2.4		2.5	2.2	4.4	2.9	2.9	2.2
DL	7.0	7.5	8.6	8.7	9.5		8.4	8.2	8.4		8.7	8.4	14.7	9.3	9.5	8.0
HV	41.2	38.7	39.3	39.7	50.5		38.8	34.0	35.3		39.0	39.0	63.3	37.4	36.9	35.5
TV	27.4	28.1	33.9	35.6	35.0		27.5	34.0	30.3	35.0	28.5	28.5	48.1	33.8	33.9	28.0
EL	6.4	7.1	11.6	10.5	8.5	13.3	9.3	10.0			11.2	11.0	16.0	11.0	11.5	8.8
EW			7.9	7.5			8.0	7.9			8.3	8.2	11.7	7.7	9.4	7.2
TL	3.2	3.5	4.9	4.8			4.1	4.4		4.2	5.0	4.9	7.6	4.4	5.1	4.9
RL	26.2	26.6	32.0	32.2	36.8		27.7	30.8	31.6	34.0	29.7	30.5	50.0	33.9	33.1	27.2
MCIII	25.1	25.5	30.7	30.0	34.0	45.1	25.6	28.8	29.3	33.0	28.1	29.0	47.8	31.6	32.4	26.3
PI	10.2	10.1	11.2	11.5	12.5	17.3	9.2	11.3	12.0	12.6	10.5	10.1	19.2	12.3	12.5	10.5
PII	7.8	7.9	9.5	11.2	10.3	10.5	7.6	9.2	9.7	11.3	8.5	9.0	15.1	10.8	10.3	8.7
PIII			6.3	6.3	7.2		5.1	6.3	6.6	5.4	6.3	6.4	13.1	7.4	5.8	6.3
TIB	10.3	10.4	14.2	13.5	16.4		11.0	12.7	8.3	13.2	11.8	11.8	22.0	13.1	12.7	11.7
PL	4.7	4.5	6.9	6.7	6.5		5.2	6.3	6.3	6.6	5.0	5.1	8.5	6.6	6.5	5.2

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